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The Morphology and Relationships of *Australochelys*, an Early Jurassic Turtle from South Africa

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ABSTRACT

Australochelys from the Early Jurassic Elliot Formation of South Africa is the oldest African turtle. Known only from the skull and a shell fragment, *Australochelys* has many primitive chelonian characters in common with the Late Triassic *Proganochelys,* such as a large interpterygoid vacuity and a lacrimal foramen. *Australochelys* has large orbits and a ventral basioccipital tubercle, characters that only occur in *Proganochelys.* However, because *Australochelys* has a series of advanced characters in common with the Casichelydia, it is more closely related to the Casichelydia (Cryptodira plus Pleurodira) than to *Proganochelys.* These characters include a sutured basipterygoid articulation and middle ear region partially enclosed laterally. *Australochelys* is hypothesized as the sister taxon to the Casichelydia; together they form the Rhaptochelydia. The relationships of *Australochelys* show that the beginning stages of the unusual turtle hearing mechanism evolved before the origin of the modern turtle groups. Akinesis preceded or accompanied the enclosure of the hypertrophied middle ear region in the early evolution of the hearing mechanism.

INTRODUCTION

Australochelys, the oldest turtle from Africa, reveals an important stage in the early history of turtles. *Australochelys* was recently described in a short paper (Gaffney and Kitching, 1994) that did not include a detailed morphological description or extended

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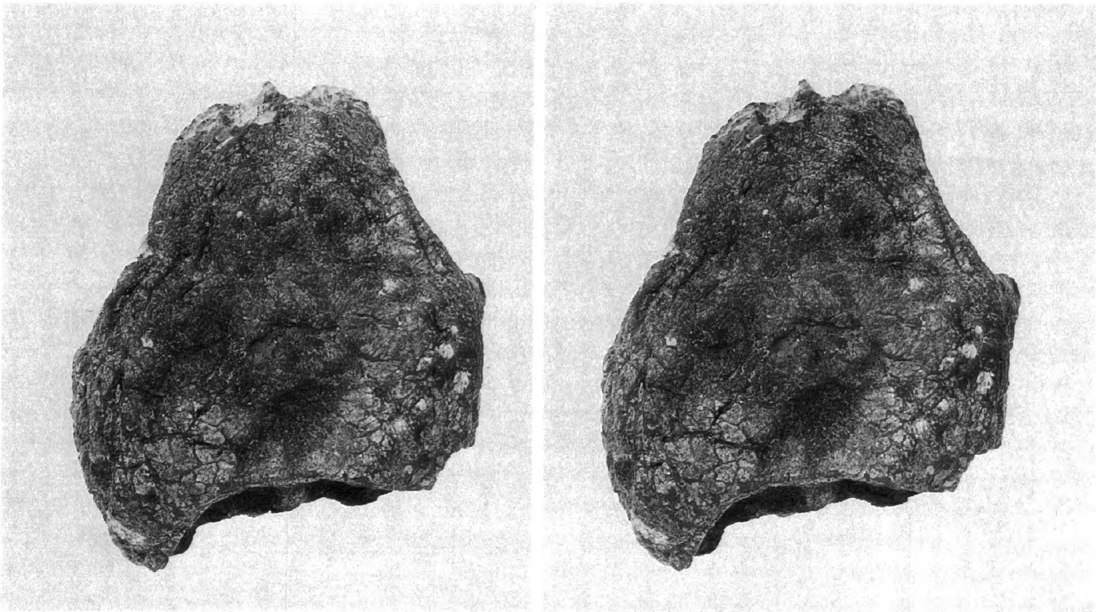

Fig. 1. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Dorsal view of skull. Stereophotograph. See fig. 3A for key.

character discussion. The purpose of this paper is to provide more descriptive information and character discussions.

The significance of *Australochelys*, as interpreted here, is that it is advanced over *Proganochelys* but lacks derived characters of either Cryptodira or Pleurodira. In addition to Gaffney and Kitching (1994), relevant

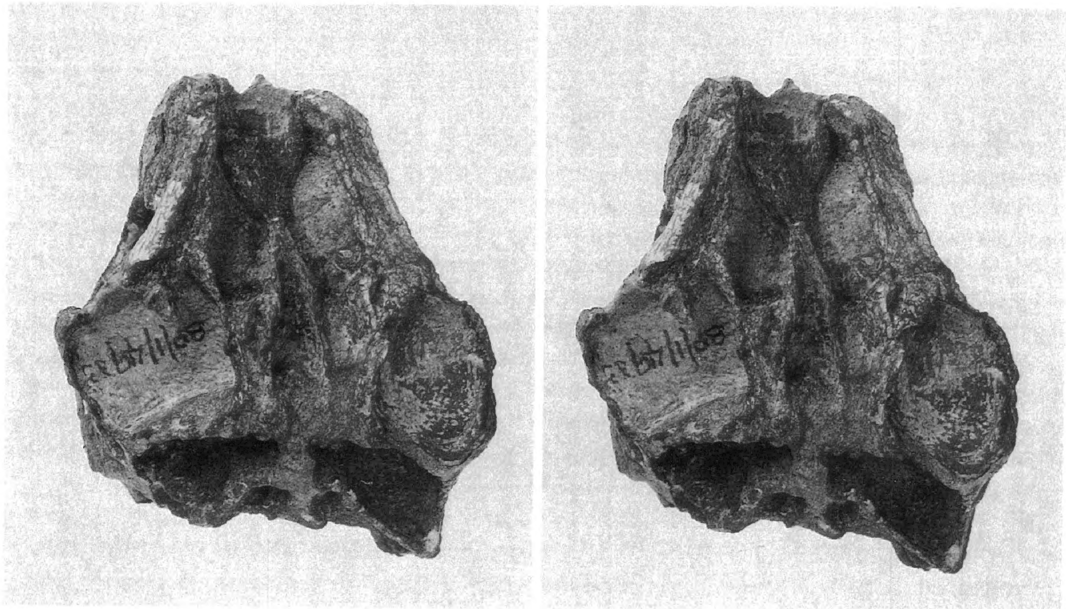

Fig. 2. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Ventral view of the skull. Stereophotograph. See fig. 3B for key.

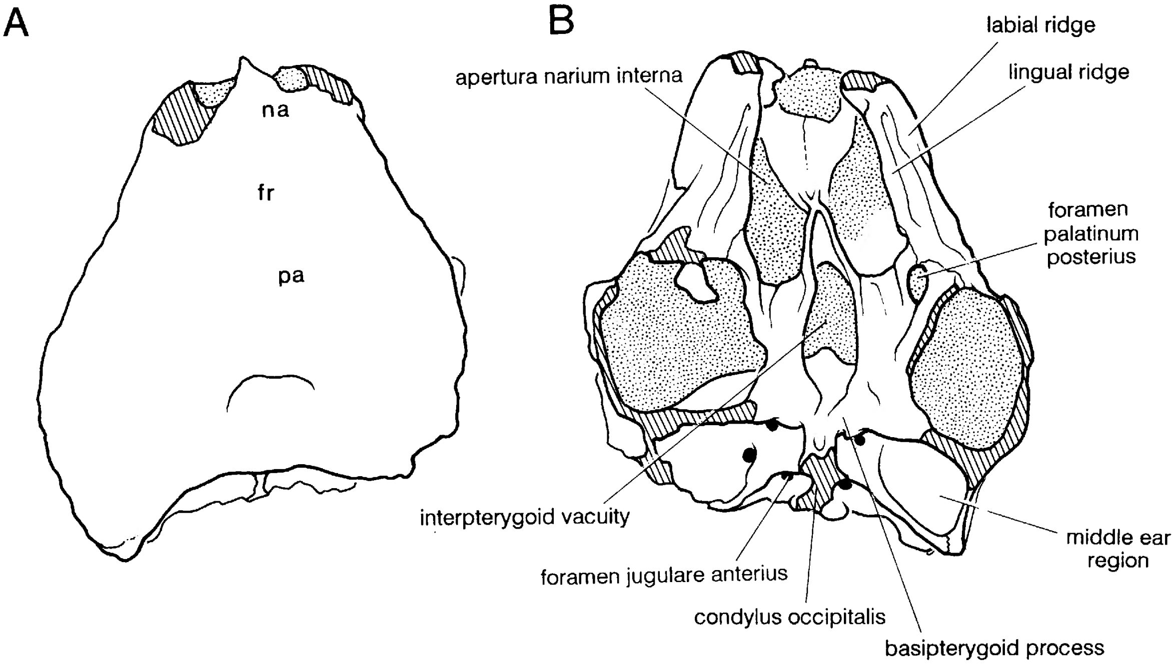

Fig. 3. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. **A.** Dorsal view of skull. **B.** Ventral view of skull.

background papers are: Gaffney (1990) for *Proganochelys,* Gaffney et al. (1987) for the earliest cryptodire, *Kayentachelys,* and Gaffney and Meylan (1988) for turtle phylogeny in general. The following skull description of *Australochelys* assumes some familiarity with the skull of *Proganochelys* (Gaffney, 1990) and general turtle skull morphology as presented in Gaffney (1979). The descriptive section here follows the order in Gaffney (1979).

Before the discovery of *Australochelys,* the oldest known African turtle was the fragmentary specimen identified by Nesbitt and Bond (1972) as a turtle from the Gokwe Formation of Zimbabwe. At that time it was questionably dated as Late Jurassic. More recently these and other turtle specimens from the Gokwe Formation of Zimbabwe have been reinterpreted as being more likely Late Cretaceous in age (M. Raath, personal commun. to J. Kitching, August 1993). At present, the next oldest known African turtles are the Early Cretaceous pleurodires summarized in de Broin (1989). This represents a gap of some 60 million years, between *Australochelys* and the Early Cretaceous pleurodires.

Acknowledgments

We are most grateful to Mr. I. van Rooyen of the farm Bormansdrift for his kindness, hospitality, and for permitting one of us (J.K.) access to his land to collect fossils. Dr. M. A. Raath helped with information on the Gokwe Formation. Dr. B. S. Rubidge, director of the Bernard Price Institute, very graciously opened the facilities and collections of that institution to one of us (E.G.). The high quality of the figures is due to the skills of F. Ippolito, E. Heck (fig. 25), and C. Tarka (fig. 19). The senior author is particularly grateful to A. Schermerhorn for improving the manuscript and assisting in its preparation.

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Abbreviations

BP Bernard Price Institute, Johannesburg, South Africa

MB	Museum für Naturkunde, Berlin, Germany
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
bo	basioccipital
bs	basisphenoid
ex	exoccipital
fr	frontal
ju	jugal
mx	maxilla
na	nasal
op	opisthotic
pa	parietal
pal	palatine
pf	prefrontal
pm	premaxilla
po	postorbital
pr	prootic
pt	pterygoid
qj	quadratojugal
qu	quadrate
so	supraoccipital
sq	squamosal
vo	vomer

SYSTEMATICS

ORDER TESTUDINES

DIAGNOSIS: As in Gaffney and Meylan (1988).

Rhaptochelydia Gaffney and Kitching, 1994

ETYMOLOGY: *rhaptos* (not "rhaptors" Gaffney and Kitching, 1994, in error), Greek for "sewn" in allusion to the sutured basipterygoid articulation; *chelys,* Greek for "turtle."

EMENDED DIAGNOSIS: Posterior margin of temporal roof extends over opisthotic; palatal teeth few or absent; basipterygoid articulation closed (sutured); cranioquadrate space a well-defined foramen or canal, the canalis cavernosus, not an open space; stapes probably articulating with a tympanic membrane, not with the quadrate; ventral ridge on opisthotic; distal end of opisthotic covered laterally by squamosal and/or quadrate; paroccipital process of opisthotic tightly sutured to braincase; crista supraoccipitalis a distinct vertical sheet of bone.

DISCUSSION: This taxon, Rhaptochelydia, is defined to consist of *Australochelys* plus Casichelydia.

FAMILY AUSTRALOCHELYIDAE Gaffney and Kitching, 1994

Australochelys Gaffney and Kitching, 1994

TYPE SPECIES: *Australochelys africanus* Gaffney and Kitching, 1994.

KNOWN DISTRIBUTION: Early Jurassic, one locality in Orange Free State, South Africa.

ETYMOLOGY: *australos,* Greek for "south"; *chelys,* Greek for "turtle."

DIAGNOSIS: As for species.

Australochelys africanus Gaffney and Kitching, 1994

TYPE SPECIMEN: Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa, BP/1/4933; consists of a skull without lower jaws and a fragment from the bridge area of the shell.

LOCALITY: Bormansdrift (133), Clocolan District, Orange Free State, South Africa. Map sheet: 1:50,000 2827 CD Mekoatlengsnek 28°57′33″S, 27°26′05″E (Kitching and Raath, 1984).

HORIZON: Tritylodon Acme-Zone, (middle) Elliott Formation, Early Jurassic (Olsen and Galton, 1984).

COLLECTOR: James W. Kitching, March 1980.

ETYMOLOGY: *africanus,* from Africa.

DIAGNOSIS

(modified from Gaffney and Kitching, 1994)

Characters unique to Australochelys *among turtles*: Orbit larger in relative size than in any other turtle; lacrimal foramen at least three times larger than in *Proganochelys*; external nares elongate in contrast to all turtles; vomers arched dorsally, narrow posteriorly, and very broad anteriorly in a unique configuration.

Primitive chelonian characters found only in Proganochelys *and* Australochelys *within turtles but also found in primitive tetrapods*: Divided external nares formed by premaxillae; large interpterygoid vacuity as in *Pro-*

ganochelys; unenclosed middle ear region; a recessed, funnel-shaped, cavum tympani absent; lacrimal foramen present; recessus scalae tympani and fenestra perilymphatica absent; foramen jugulare posterius with at least a medial edge absent; cultriform process present.

Advanced chelonian characters found only in Australochelys *and* Casichelydia *(Cryptodires plus Pleurodires)*: Basipterygoid articulation sutured; stapes probably does not articulate directly with quadrate but may have attached to a tympanic membrane supported by the acute posterior edge of the quadrate; distal end of opisthotic covered by quadrate; canalis cavernosus a well-defined canal; few or no palatal teeth; crista supraoccipitalis a distinct vertical sheet of bone; temporal roof extends posteriorly over opisthotic.

DESCRIPTION

PRESERVATION

The type specimen of *Australochelys africanus* is preserved in a highly indurated, hematite-cemented, fine-grained sandstone. Postmortem cracking and hematite infiltration have caused minute reorientation of bone trabeculae and loss of fine structural detail in most areas. There has been lateral deformation of the skull in which the anterior part has been pushed to the right, in dorsal view, with respect to the posterior part. The skull roof is the most fractured; the palate and braincase retain finer detail. The postmortem hematite infiltration has destroyed many areas with potential sutures. However, it is likely that the general absence of sutures in *Australochelys* is not only the result of preservational changes, but also because there are a number of places that seem sufficiently preserved to reveal sutures if they were present. The type skull of *Australochelys* probably had most of its sutures fused during life.

Because most sutures are not visible in *Australochelys,* we have described skull areas rather than bones. However, for the sake of practicality in the description, certain areas in *Australochelys* are assumed to consist of the same bones forming those areas in *Proganochelys* and other turtles.

DERMAL ROOFING ELEMENTS
(figs. 1, 3–6)

The nasal area of *Australochelys* is characterized by a deep snout, large fossa nasalis, and an elongate apertura narium externa. In contrast, *Proganochelys* has a relatively small snout, small fossa nasalis, and a less elongate apertura narium externa. These features in *Australochelys* are probably autapomorphic, although a large fossa nasalis is common in other amniotes and does occur in some Casichelydia. *Australochelys* has a paired apertura narium externa, with a well-developed internarial bar, as in *Proganochelys.* The internarial bar is broad dorsally, becomes narrower ventrally, but its ventral limits are not preserved. The dorsal end of the bar is pushed under the skull roof along what could be a suture. If this is a suture, it is likely that the internarial bar is formed by the premaxillae, as in *Proganochelys.* It is also possible that a crack on the midline of the internarial bar is a median suture (fig. 8).

Each apertura narium externa is roughly oval, elongate dorsoventrally. The lower limits are not complete on either side, but the general extent of the apertura can be estimated by extending the ventral edge of the skull anteriorly. The right side has the better preserved apertura narium externa.

Other than a possible premaxilla–nasal contact on the midline, there are no visible sutures delimiting the nasal bone in *Australochelys.* The anterior part of the skull roof, formed by the nasal in *Proganochelys,* is more convex and curved in *Australochelys* than in *Proganochelys.* This is related to the larger size of the fossa nasalis in *Australochelys.*

Proganochelys differs from all Casichelydia in having a lacrimal bone and a lacrimal foramen. *Australochelys* also has a lacrimal foramen and may have a lacrimal bone as well. On the right side of *Australochelys* (fig. 5) there are cracks in about the same places as those in the lacrimal sutures in *Proganochelys.* However, none of these can be confirmed as sutures when examined microscopically.

The lacrimal foramen is oval and unusually large in *Australochelys,* about three times larger than in *Proganochelys.* The internal fossa nasalis in *Australochelys* is filled with

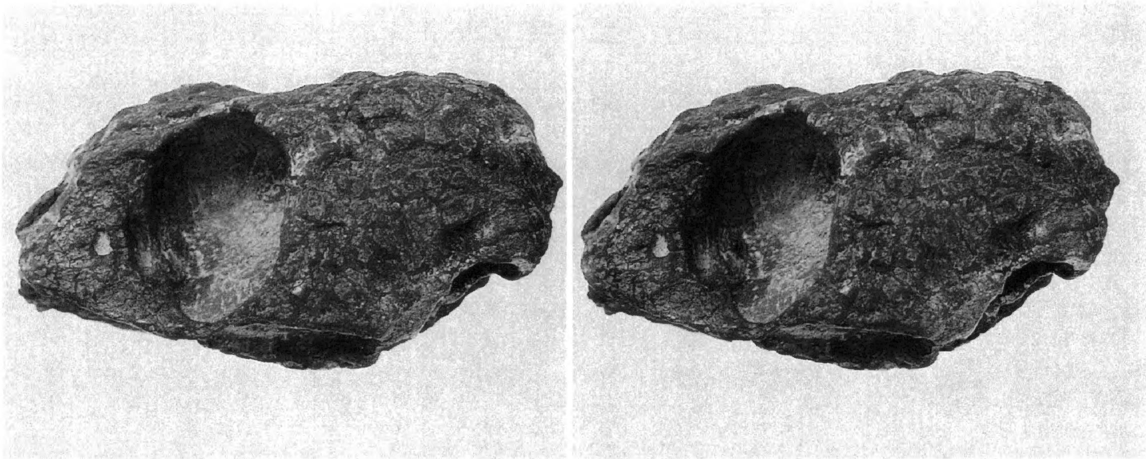


Fig. 4. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Left lateral view of skull. Stereophotograph. See fig. 6A for key.

matrix, so the presence or absence of a lacrimal groove cannot be determined.

In the right orbit of *Australochelys* there is a small hole dorsomedial to the lacrimal foramen (figs. 5, 6). This is possibly an additional lacrimal foramen, as seen in *Proganochelys* SMNS 15759 (Gaffney, 1990). Because of its irregular shape and broken edges, we interpret it as an artifact of preservation. On the left side (figs. 4–6) anterior to the orbital margin is another opening that also seems to be due to breakage.

The frontal and parietal bones (figs. 1, 3) presumably make up the central area of the skull roof in *Australochelys*, but no sutures are visible, not even midline sutures. The area of the presumed frontal in *Australochelys*, by comparison with *Proganochelys*, has a low convexity on the midline, an area that is flat in *Proganochelys*. There is also a small-

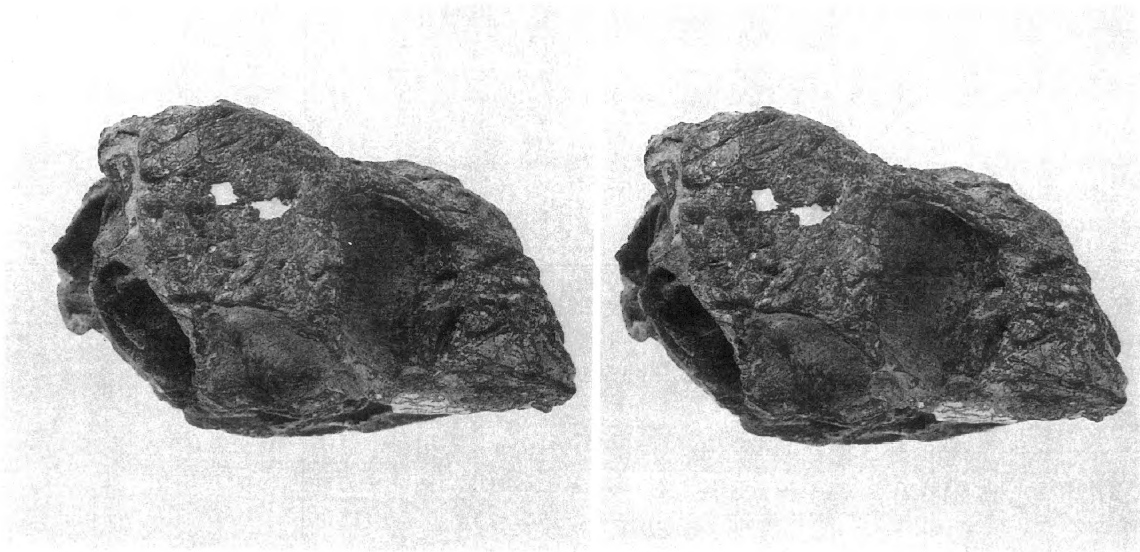


Fig. 5. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Right lateral view of the skull. Stereophotograph. See fig. 6B for key.

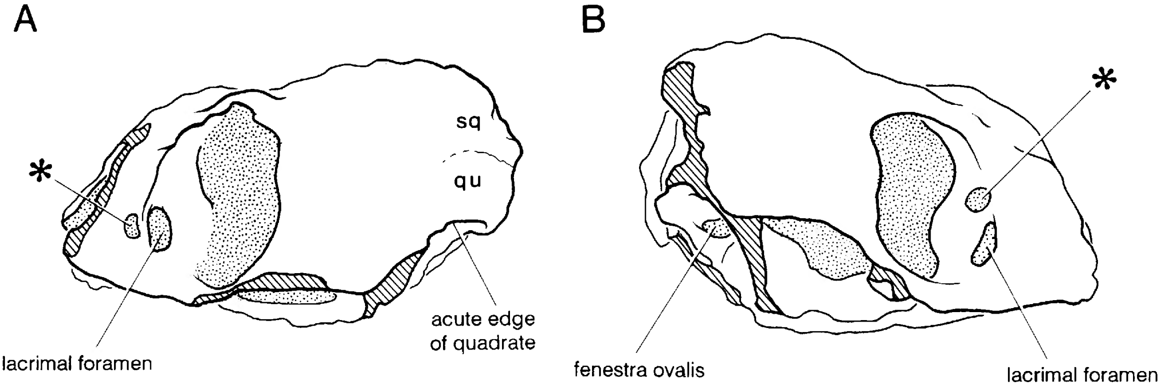


Fig. 6. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. **A.** Left lateral view of skull. **B.** Right lateral view of skull. The structures marked with an asterisk (*) are interpreted as artifacts, not premortem foramina.

er convexity in the region of the presumed parietal just behind the first convexity. It is possible that the second convexity is comparable to scale area 10 in *Proganochelys* (Gaffney, 1990: fig. 17). Just behind the second convexity in *Australochelys* there is a shallow concavity, and this may be comparable to scale area 8 in *Proganochelys,* also a poorly defined concavity. However, these are the only possible similarities between assumed scale areas in *Australochelys* and *Proganochelys.* In any case, *Australochelys* lacks definable scale areas, at least as preserved.

Australochelys lacks any indication of the supraorbital bumps, scale areas 1–4, seen in *Proganochelys.* On both sides of *Australochelys* the supraorbital margin is depressed from the level of the skull roof. No sutures delimiting possible prefrontal or postorbital bones are visible on the dorsal surface or on the ventral surface of the skull roof that is visible within the fossa orbitalis.

The fossa orbitalis in *Australochelys* (fig. 11) is unusually large, relatively larger than that in any other turtle, including *Proganochelys.* It is not possible to identify the circumorbital bones, but the skull roof is relatively thin in the roof of the fossa orbitalis. The bone in the lower margin of the fossa orbitalis (presumed maxilla) is also thin. The orbit seems to be as large as morphologically possible in a skull of this size.

Both orbits of *Australochelys* have the anterior wall of the fossa orbitalis exposed. In *Proganochelys* this wall is formed by the ventral process of the prefrontal, and that is presumed to be the case in *Australochelys.* The medial edge of the process in *Australochelys* can be seen on the left side and it is larger and more extensive than the prefrontal process in *Proganochelys.*

A distinct foramen orbitonasale is not visible in *Australochelys,* although there are poorly preserved indentations in the correct position in both orbits that could be interpreted as the foramina.

The postorbital region of the skull roof (figs. 4–6) is preserved on both sides of *Australochelys,* but it is more complete on the left side. It is possible that postorbital–jugal sutures are represented by cracks in the orbital margins on both sides. They are in positions slightly higher than in *Proganochelys.* There are no other possible sutures. The postorbital section of the skull, between the orbit and the quadrate, is shorter in *Australochelys* than in *Proganochelys.*

The temporal emargination in turtles has had a complex history (see Gaffney, 1979, for discussion), and its early history as seen in *Proganochelys* and *Australochelys* is no exception (fig. 10). In *Proganochelys* the supraoccipital and opisthotic are broadly exposed in dorsal view, whereas in *Australochelys* the posterior margin of the skull roof extends backward to nearly cover them in dorsal view. In lateral views the distal end of the opisthotic in *Australochelys* is covered,

TABLE 1
Comparative Skull Measurements (in cm)

	Australochelys	*Proganochelys*	
	BPI/1/4933	SMNS 16980	MB.1910.42.2
Premaxilla condyle length	9.1	9.7	13.3
Premaxilla–posterior edge of skull roof	9.0	8.1	12.0[a]
Width of skull over orbits	5.0	7.0	7.4[b]
Width of skull at mandibular articulation	8.7	8.1	7.6[b]
Width of maxillary triturating surface	1.0	0.6	1.2
Length of triturating surface	3.9[a]	4.4	7.2 (L)
Width of orbit	3.4 (L)	3.2 (R&L)	3.5 (R) 3.8 (R)
Distance between posterior margin of orbit and posterior edge of quadrate	3.3 (L)	3.9 (R) 3.5 (L)	5.8 (L) 3.8 (L)
Distance between anterior margin of orbit and posterior margin of apertura narium externa	1.9(L)	2.0	2.9

[a] One margin measured is a broken edge.
[b] Measurement obviously influenced by postmortem deformation.

whereas it is exposed in *Proganochelys*. In *Proganochelys* the temporal roof is complete and unemarginated in comparison with most turtles. However, *Australochelys* has a more extensive skull roof, and we think that this is best interpreted as the primitive condition for Casichelydia, but not at the level of Testudines. Because the less extensive temporal roof of *Proganochelys* is hypothesized as the primitive condition for Testudines, the more extensive roof of *Kayentachelys* (Gaffney et al., 1987) suggests that the more extensive *Australochelys* condition is primitive for Casichelydia.

The posterior margin of the skull roof is nearly complete on the left side and the medial portion is complete on the right side of *Australochelys*. There is a distinct recessed lower margin or shelf along the posterior margin of the skull roof in *Australochelys*, which is not present in *Proganochelys*. In *Proganochelys* there is a raised tubercle, scale area 9, along the posterolateral edge of the temporal margin. This scale area is formed by the supratemporal bone. In *Australochelys* there is no sign of a raised scale area along the temporal margin, which may indicate the absence of the supratemporal, as in all other turtles. However, the absence of sutures in *Australochelys* makes this impossible to confirm.

Palatal Elements
(figs. 2, 3, 12–14, 21, 22)

Most of the premaxillary region of the *Australochelys* skull is missing due to prefossilization breakage (fig. 2). If the internarial bar is formed from the premaxilla, then this would be the only part of that bone preserved.

Most of both maxillae are present in *Australochelys* and a few possible sutures are interpretable on the ventral surface (figs. 2, 3, 21, 22). In lateral view no sutures are visible, but the maxilla presumably forms the ventral margin of the skull anteriorly. This margin is an eroded edge on both sides of the skull, but it is unlikely that very much bone is missing. None of the original margin is preserved. Thus, the actual extent of the bone is unknown, but based on the angle and thickness of the preserved surfaces, the original labial ridge would probably have been similar to that in *Proganochelys*.

The triturating surface in *Australochelys* is narrow, much as in *Proganochelys* but wider posteriorly than in that form (figs. 19–22). The lingual ridge is distinct but low, as in *Proganochelys*, but differs from *Proganochelys* in becoming lower posteriorly.

On the right side there is what appears to be the palatine–maxilla suture running anteromedially from the foramen palatinum

posterius parallel to the triturating ridges (figs. 2, 3). This contact can also be seen on the left side, adjacent to the foramen palatinum posterius. Also on the left side, the contact of the palatine with the pterygoid just lateral to the foramen palatinum posterius is visible. If these interpretations are correct, the foramen palatinum posterius is formed primarily by the palatine and pterygoid as in *Proganochelys* (figs. 19–22).

It is possible that a midline suture is present and that the vomer in *Australochelys* may be paired. Even though this cannot be confirmed, we describe the vomer as if it were paired. Anteriorly, the vomer has a free, but broken, margin as preserved; its presumed contact, the premaxilla, is missing. There is no evidene of teeth on the vomer of *Australochelys*. The vomer in *Australochelys* is a very unusually shaped element that curves dorsally well above the level of the triturating surfaces (figs. 2, 3, 23). In *Proganochelys* the vomer is somewhat above the rest of the palate, but not to the extent seen in *Australochelys*. The vomer in *Proganochelys* is a narrow, relatively straight-sided element, similar to that in other turtles; however, in *Australochelys* the area presumably formed by the vomer is only narrow posteriorly where it has a small contact with the presumed palatine. The vomer is very wide anteriorly with an anteroventrolateral process reaching to the maxilla.

Parts of the areas interpreted as palatines (figs. 2, 3, 21, 22) are preserved on both sides in *Australochelys*, although the extent of missing bone is not determinable. The presumed palatine in *Australochelys* is unusual for any turtle, including *Proganochelys*. In most turtles the palatine is a flat, horizontal element that forms the roof of the palate. In *Australochelys*, however, the palatine is reduced to a series of more vertical plates or struts, and the area usually covered by the palatine contains an unusually large apertura narium interna. On the midline, what is presumed to be palatine is a nearly vertical sheet of bone that meets the other palatine to form a V-shaped structure. This structure is concave ventrally and widens posteriorly as the interpterygoid vacuity (figs. 12–14). This V-shaped strut seems to be comparable with a tooth-bearing ridge formed by the pterygoid in *Proganochelys* (Gaffney, 1990). In *Proganochelys* the pterygoids extend anteriorly on the midline to prevent medial contact of the palatines. This condition could well be the case in *Australochelys*, but there are no sutures to allow identification of the bones involved.

Laterally, the palatine can be identified contacting the maxilla and forming the lateral wall of the apertura narium interna. This contact also consists of a curved, nearly vertical sheet of bone rather than the flat plate seen in other turtles. Between the two vertical sheets there are numerous, more horizontal fragments of bone lying in matrix well dorsal to the level of the triturating surfaces. These fragments probably represent a thin, curved portion of the palatine that connected the more medial and the more lateral sheets (figs. 2, 21).

The apertura narium interna in *Australochelys* (figs. 2, 3) is unusual in being very large and confluent anteriorly at the level of the triturating surfaces. The high, dorsally placed vomers only separate the internal nares above the level of the palate. The V-shaped sheet of palatine/pterygoid posterior to the vomers ends ventrally at the level of the triturating surfaces and separates the nares posteriorly. As preserved, the apertura narium interna extends posteriorly lateral to the V-shaped bone to the position of the foramen palatinum posterius. The apertura narium interna of *Australochelys* is much more extensive than in *Proganochelys* or in *Kayentachelys* and other primitive turtles. There is evidence that bone (probably palatine) formed a dorsal, choanal trough for at least some of the opening, as shown in figure 21.

Palatoquadrate Elements
(figs. 2, 3–6, 12–18)

Parts of what are presumed to be the quadrates are preserved on both sides of *Australochelys* (figs. 4–6); the left side is more complete, but both sides lack the ventral portion and condylus mandibularis. On the left side some of the dorsal contact of the quadrate with the squamosal can be seen. In contrast to *Proganochelys*, the distal end of the opis-

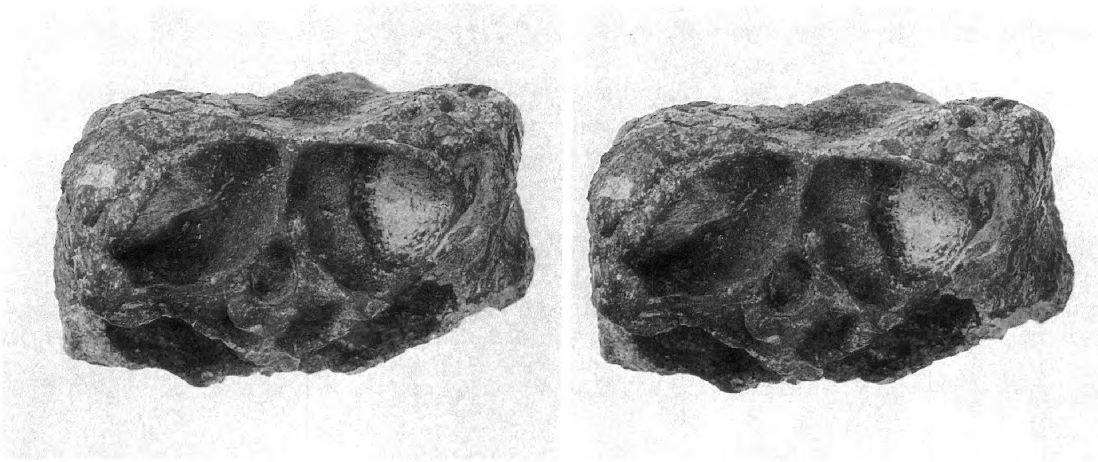


Fig. 7. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Occipital view of skull. Stereophotgraph. See fig. 9A for key.

thotic in *Australochelys* is covered in lateral view by this area of squamosal and quadrate contact. The lateral covering of the opisthotic is an advanced feature of the Rhaptochelydia, *Australochelys* plus Casichelydia.

The posterior margin of the quadrate in *Proganochelys* is a relatively thick, broadly curved surface (figs. 10, 23). In *Australochelys* the posterior free edge of the quadrate is an acute margin, quite different from *Proganochelys* (figs. 6A, 14A). This edge in *Australochelys* is preserved only on the left side and its lower portions are missing, but it is curved in lateral view so that it appears to have been C-shaped originally. There is no development of a recessed, funnel-shaped cavum tympani as seen in Casichelydia. In Casichelydia the distal end of the columella auris attaches to the tympanic membrane, whereas in *Proganochelys* and primitive tetrapods the stapes articulates with the quadrate. A stapes is absent in *Australochelys,* so its distal articulation is not known; however, it is unlikely that it articulated with the quadrate, as in

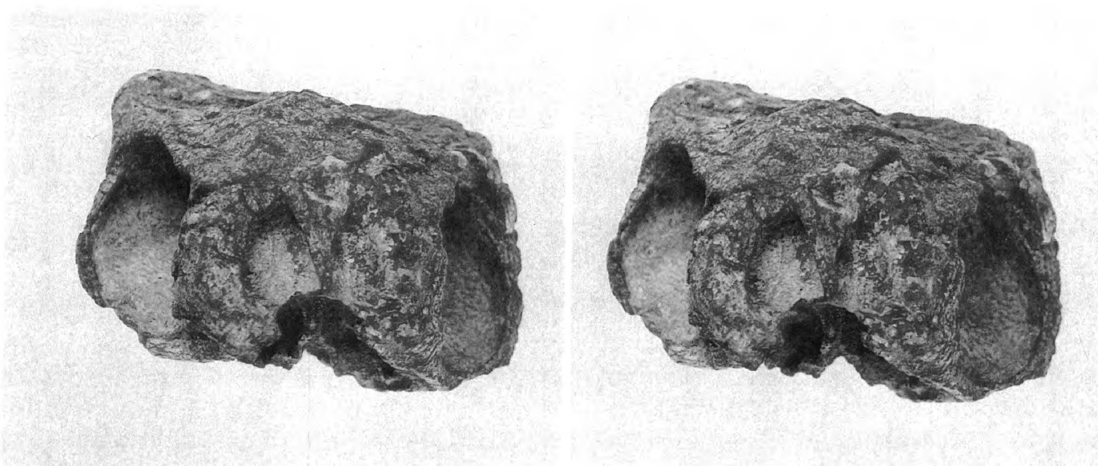


Fig. 8. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Anterior view of skull. Stereophotograph. See fig. 9B for key.

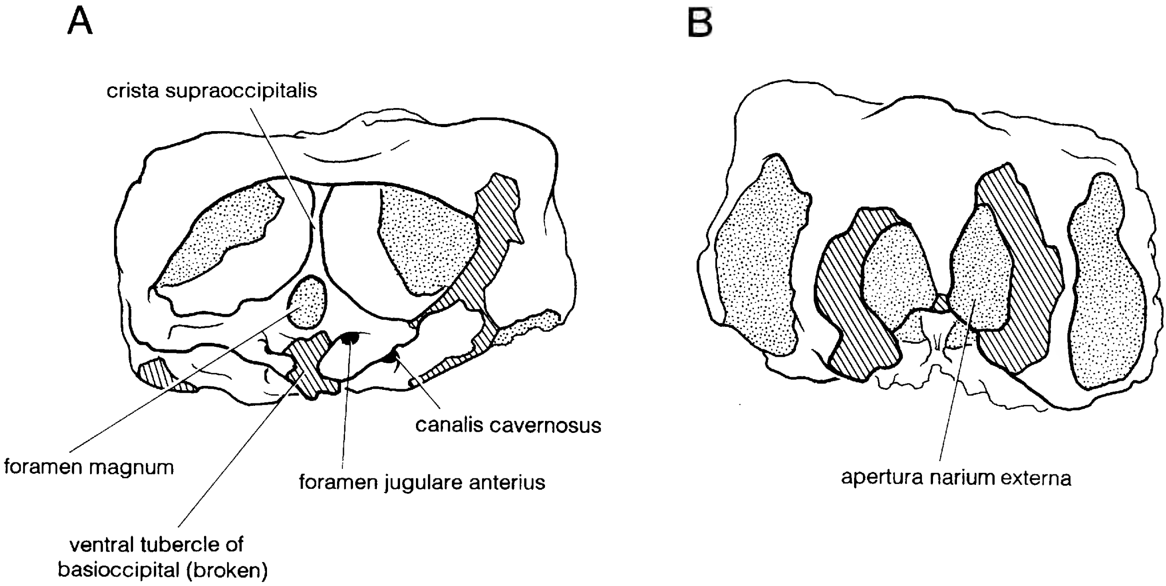


Fig. 9. **A.** Occipital view of skull. **B.** Anterior view of skull.

Proganochelys. The area on the quadrate where the stapes articulates in *Proganochelys* is deeply recessed and far from the presumed tympanic margin in *Australochelys.* Thus, it is likely that the distal end of the stapes in *Australochelys* attached to the tympanic membrane.

Australochelys agrees with *Proganochelys* in completely lacking an antrum postoticum and a recessed cavum tympani of the sort seen in Casichelydia (fig. 23). It is difficult to be sure where the tympanic membrane attached in *Australochelys* because there is no clear attachment edge. However, the presumed quadrate in *Australochelys* has a recessed marginal area paralleling the C-shaped posterior edge, and this could represent an incipient cavum tympani, if the tympanic membrane attached along its proximal margin.

Most of both presumed pterygoids (figs. 2, 3, 12–18, 21–23) are preserved in *Australochelys.* There is a probable suture with the maxilla on the left side, but no other pterygoid sutures are visible. The left pterygoid is more complete than the right, but both are missing some bone. The right pterygoid is missing most of the processus pterygoideus externus and only an isolated fragment of bone contacts the maxilla and forms part of the foramen palatinum posterius. The right pterygoid contacts the maxilla anterolaterally in front of the foramen palatinum posterius and apparently contacts the jugal lateral to the foramen. The foramen palatinum posterius of *Australochelys* is less than half the size of that in *Proganochelys.*

Both pterygoids in *Australochelys* have incomplete temporal fossa margins, but the left pterygoid does not seem to be lacking very much. There is no indication of a cryptodiran processus pterygoideus externus or a pleurodiran processus trochlearis pterygoideus. The size and shape of the broken edge instead suggest a downturned margin like that in *Proganochelys.*

The anterior or palatine process of the pterygoid cannot be delimited by sutures, but the pterygoid may form part or all of the V-shaped sheet lying behind the vomers on the midline (figs. 2, 3, 8, 12–14). The space enclosed by this sheet anteriorly, and by the main body of the pterygoid posteriorly, is the interpterygoid vacuity, which is found in other turtles only in *Proganochelys* and *Kayentachelys* and, now, *Australochelys* (fig. 10). The interpterygoid vacuity in *Australochelys* is about the same length as in *Proganochelys* but wider than in *Proganochelys.* In *Kayentachelys* the vacuity is much smaller than in either *Aus-*

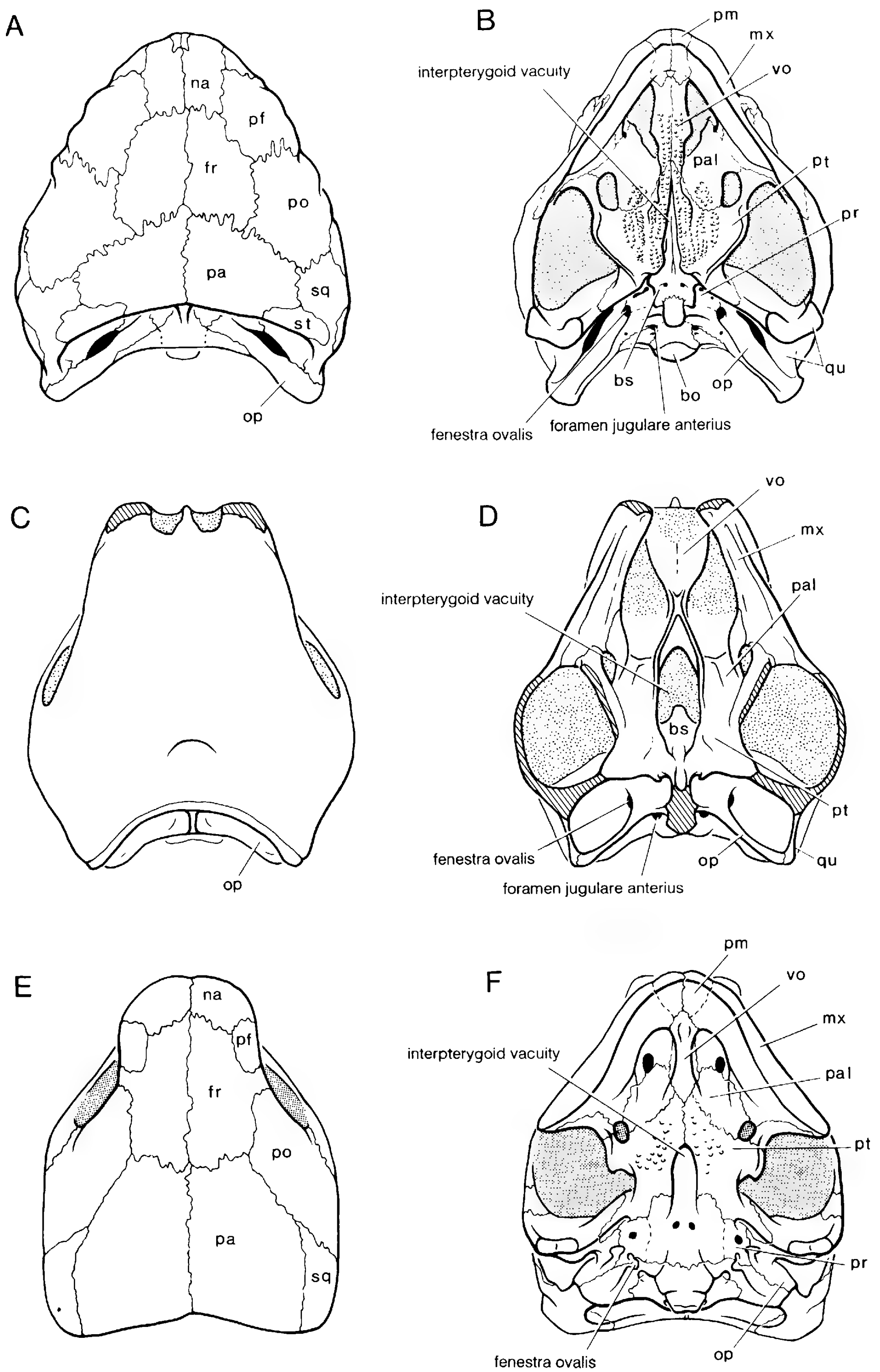


Fig. 10. Comparative views of turtle skulls. **A, B.** *Proganochelys quenstedti,* Late Triassic, from Gaffney, 1990. **C, D.** *Australochelys africanus,* Early Jurassic. **E, F.** *Kayentachelys aprix,* Early Jurassic, from Gaffney et al., 1987. A, C, E are dorsal views; B, D, F, ventral views.

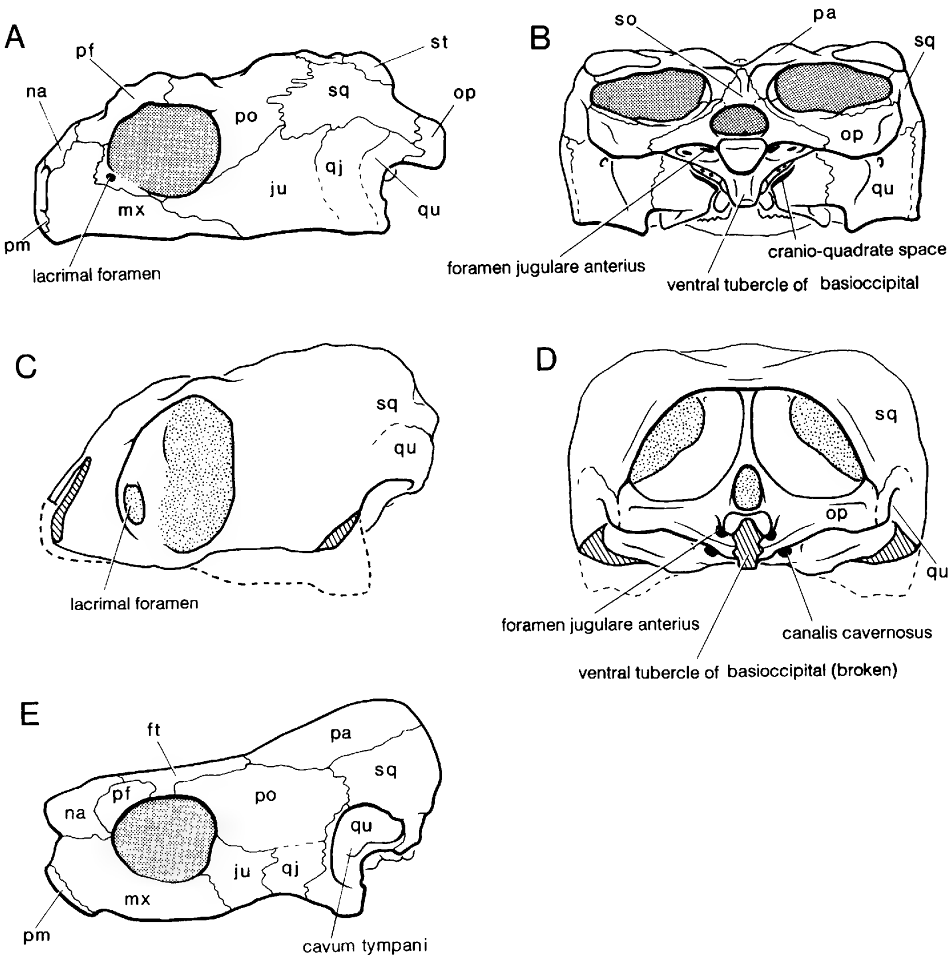


Fig. 11. Comparative views of turtle skulls. **A, B.** *Proganochelys quenstedti,* Late Triassic from Gaffney, 1990. **C, D.** *Australochelys africanus,* Early Jurassic. **E.** *Kayentachelys aprix,* Early Jurassic, from Gaffney et al., 1987. A, C, and E are lateral views; B and D, occipital views.

tralochelys or *Proganochelys*; this is presumably a casichelydian synapomorphy.

In *Australochelys* a ridge forms the lateral margin of the interpterygoid vacuity that is continuous with the V-shaped sheet. This ridge is in roughly the same position as the medialmost row of palatal teeth in *Proganochelys* (fig. 10). It is possible that this ridge in *Australochelys* also had denticles, but none are preserved.

Lateral to the ridge forming the margin of the interpterygoid vacuity, the pterygoid (possibly also the palatine) is relatively flat. On this flat portion there is a low ridge that parallels the more medial ridge. On the left side of the skull the more anterior part of the ridge is preserved, but on the right side the ridge is longer and extends the length of the interpterygoid vacuity. This more extensive ridge on the right side bends and parallels the edge of the interpterygoid vacuity. The ridge is roughly comparable to the central set of tooth rows in *Proganochelys.* Close examination of this ridge in *Australochelys* reveals small bumps that may be worn denticles, but the preservation is too poor to allow a definite conclusion. In any case, *Australochelys* lacks the extensive tooth rows seen in *Proganochelys,* although some teeth may have been present along the ridges described above. This reduction in tooth rows appears to be a synapomorphy for the Rhaptochelydia.

One of the most important indicators of the relationships of *Australochelys* is the con-

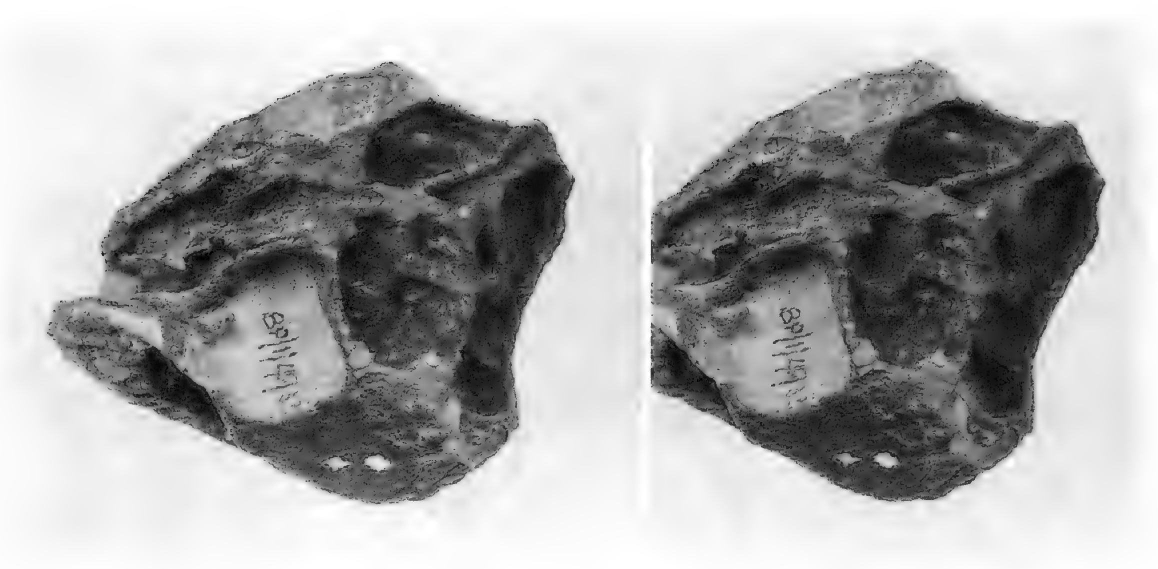


Fig. 12. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Ventrolateral oblique view of right side of skull. Stereophotograph. See fig. 14A for key.

dition of the basipterygoid articulation (fig. 23). In *Proganochelys* the contacts of pterygoid and basisphenoid are clearly a movable articulation as in the primitive condition for amniotes (Gaffney, 1990). In *Kayentachelys* and other casichelydians the articulation is a suture between the two bones (Gaffney et al., 1987). In *Australochelys* the basipterygoid articulation is fused with no indication of a movable joint (figs. 15–18, 21, 23). Unfortunately there is also no clearly identifiable suture to show the actual position of the contact of pterygoid and basisphenoid. Although there is minute breakage and infiltration cracks of hematite that obscure sutures in *Australochelys*, we do not think that a well-defined suture was present premortem. The bone trabeculae and lineations can be seen in a number of areas where the pterygoid–basisphenoid suture should be and there is

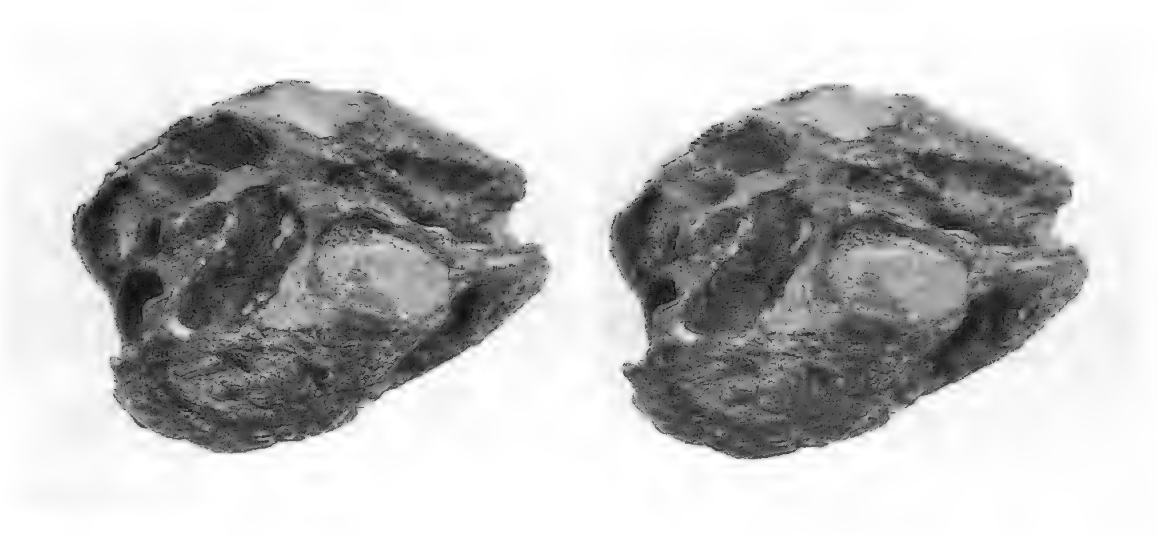


Fig. 13. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Ventrolateral oblique view of left side of skull. Stereophotograph. See fig. 14B for key.

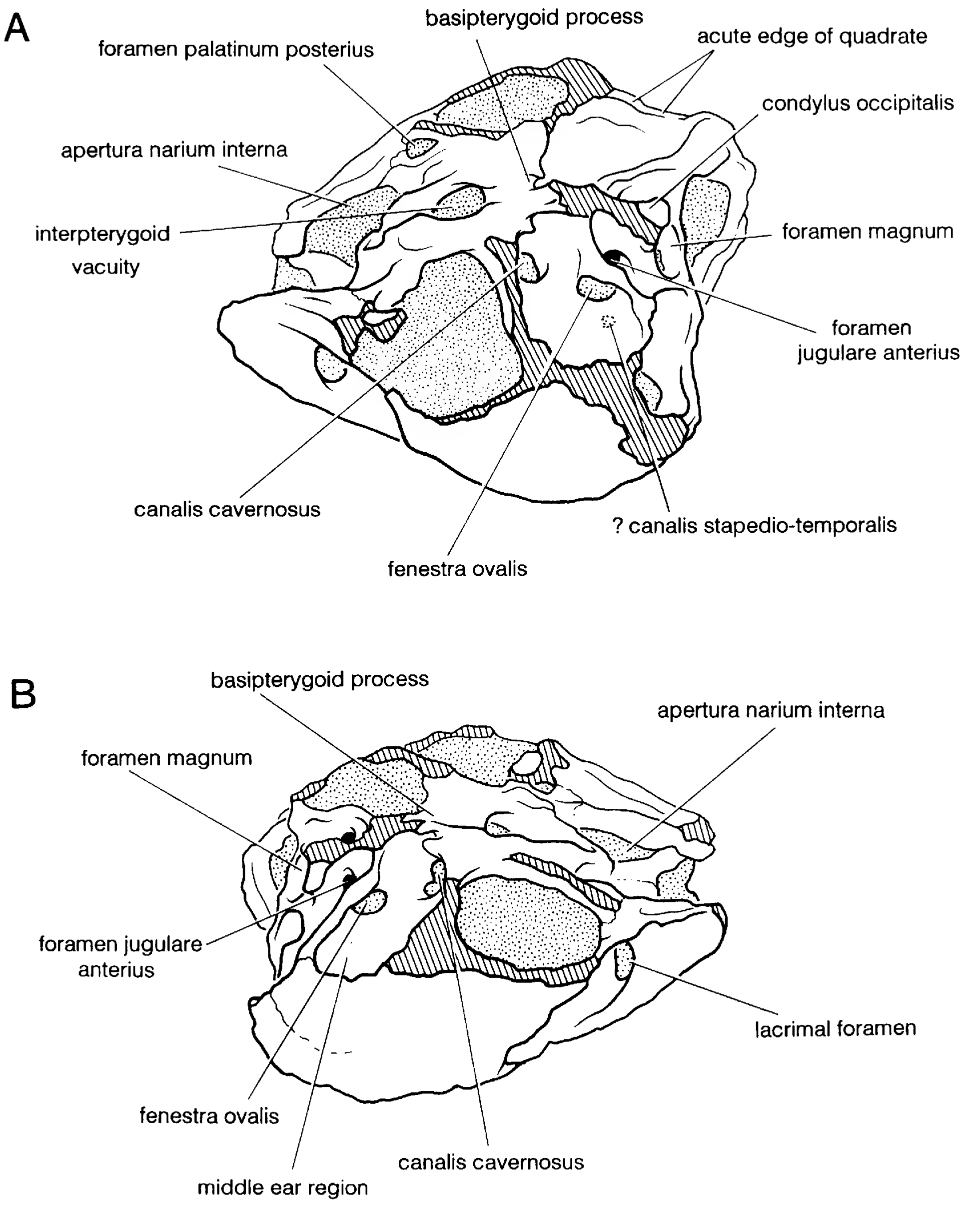


Fig. 14. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. **A.** Ventrolateral oblique view of right side of skull. **B.** Ventrolateral oblique view of left side of skull.

no indication of it. However, a likely fused sutural area can be hypothesized based on indistinct changes in trabeculae lineation and surface grooves, and this is in the approximate position of the articulation in *Proganochelys*.

The basicranial articulation is more than just fused in *Australochelys* compared with *Proganochelys*. The adjacent parts of the pterygoid and basisphenoid anterior to the articulation in *Proganochelys* are separated by a space, but in *Australochelys* bone fills the space (figs. 15, 16). This has doubled or tripled the pterygoid and basisphenoid contact area in *Australochelys* compared with *Proganochelys*. This increased contact area curves vertically and medially from the main body of the pterygoid.

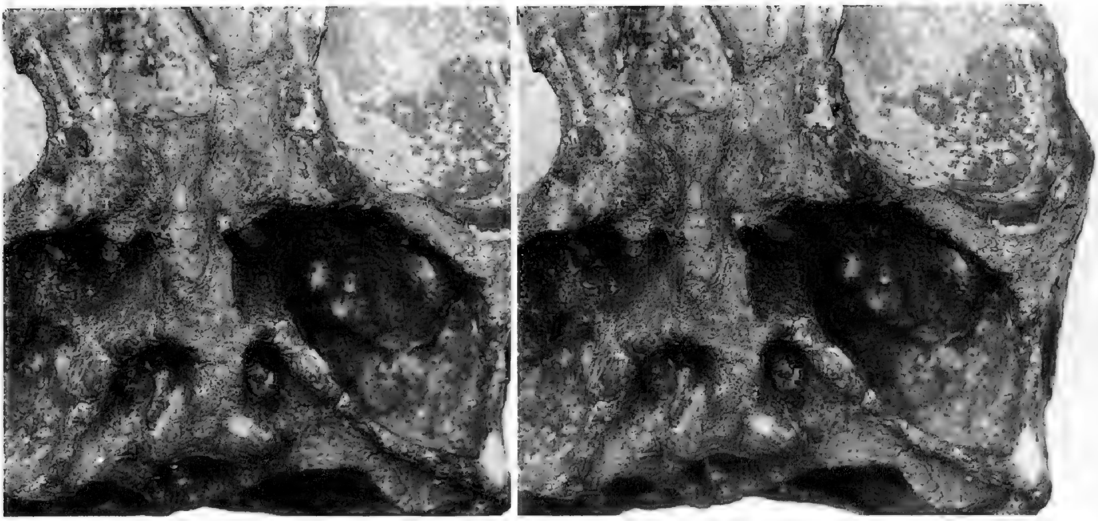


Fig. 15. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Ventral view of left ear region. Stereophotograph. See fig. 16 for key.

The quadrate ramus of the pterygoid and the pterygoid ramus of the quadrate cannot be distinguished from each other because of the absence of sutures in *Australochelys*. The two bones form a curved plate as in *Proganochelys*, with no indication of a swollen cryptodiran processus trochlearis oticum. In *Australochelys* this quadrate and pterygoid plate

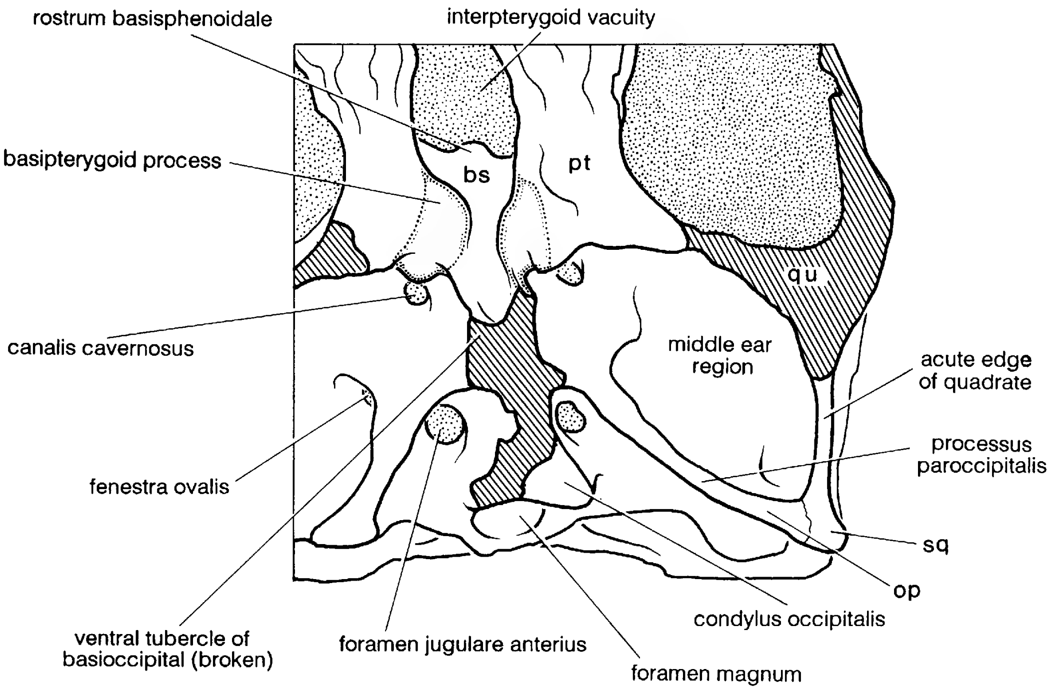


Fig. 16. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Ventrolateral view of left ear region.

forms the anterior wall of the middle ear region, and it is more enclosed than in *Proganochelys.*

The quadrate has an acute, posteriorly developed flange (figs. 4–6, 12–14) that, along with the ventrally developed opisthotic, encloses the middle ear region to a greater extent than in *Proganochelys.* This is not the cavum acustico-jugulare of Casichelydia, which includes an area walled off posteriorly by the exoccipital; instead, it is a step toward an enclosed middle ear region.

In *Proganochelys* the lateral head vein passes through a relatively open fissure formed ventrally by the pterygoid and dorsally by the prootic and opisthotic (fig. 23). In casichelydians the lateral head vein is enclosed in a canal, the canalis cavernosus. Although the area in *Australochelys* is damaged and lacks sutures, there is a well-defined foramen on each side (figs. 14, 18, 23) that is clearly a canalis cavernosus of the casichelydian type, making this character a rhaptochelydian synapomorphy.

Breakage and distortion of the canalis cavernosus on each side has made the two openings different in shape but the position is the same. Each foramen has pieces of a broken wall separating it from another more dorsal foramen so that the result is an irregular oval partially separated by broken bone (fig. 18). This second foramen may contain the facial (VII) nerve, which is contained in the cranioquadrate space in *Proganochelys.* In *Australochelys* there is so much erosion and distortion that it is likely that these two openings have become partially confluent.

A clearly defined opening for the stapedial artery cannot be found in *Australochelys.* However, there are areas of matrix on both sides without clear borders that do seem to penetrate dorsally through the otic chamber wall. These areas could be stapedial foramina (figs. 17, 18). The absence of sutures and the ambiguity of these structures prevents useful comparison, but they lie somewhat more anteriorly than the canalis in *Proganochelys.*

Braincase Elements
(figs. 7, 9, 12–18, 21–23)

The crista supraoccipitalis in *Proganochelys* is a mere ridge and virtually absent. In *Australochelys* there is a distinct crista supraoccipitals running from the underside of the skull roof to the foramen magnum. It is broken along its posterior edge, but seems unlikely that much is missing. The crista supraoccipitalis in *Australochelys* (figs. 7, 8), although more extensive than in *Proganochelys,* is not as deep or as well developed as in *Kayentachelys* or other Casichelydia.

The base of the crista supraoccipitalis, where the cavum cranii expands anteriorly to form the braincase proper, is large in *Australochelys* relative to other turtles. In *Proganochelys* this area is larger than in most casichelydians, but not as large as in *Australochelys.* This area in *Australochelys* is probably parietal as well as supraoccipital, but there are no sutures. The braincase area beneath the skull roof is expanded laterally and ends in small, posterolateral processes that curve backward to form a posteriorly opening concavity on each side of the crista supraoccipitalis (fig. 7). There is a hint of such a condition in *Proganochelys* but nothing like it in any other turtle. The concavities may be for the attachment of craniocervical muscles.

The large base of the crista supraoccipitalis could be interpreted as a *Proganochelys–Australochelys* synapomorphy. However, *Proganochelys* is not significantly larger than in many casichelydians and it seems best to interpret the *Australochelys* condition as an autapomorphy.

Much of the basioccipital in *Australochelys* is broken off in a nearly flat, oblique section. Although most of the ventral tubercle is missing, it is clear that one was present (figs. 15–18) and that it was similar in size and shape to the ventral tubercle in *Proganochelys* (figs. 19, 20). This tubercle does not occur in other turtles, nor does it occur in likely turtle outgroups, such as procolophonids, *Owenetta,* pareiasaurs, or captorhinids. This character could be interpreted as a synapomorphy that would unite *Proganochelys* and *Australochelys* and is the main contradiction to the hypothesis of *Australochelys* plus Casichelydia as a monophyletic group.

About two thirds of the condylus occipitalis in *Australochelys* (figs. 7, 9, 15–18) is broken off, but what remains is very similar to that in *Proganochelys.* The articulation is roughly triangular, being slightly wider than

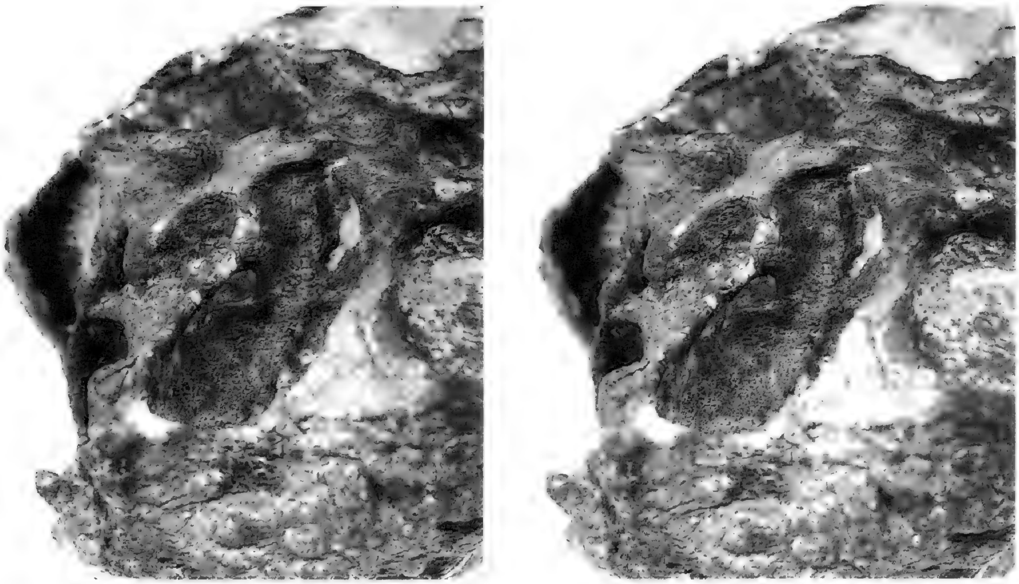


Fig. 17. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Ventrolateral oblique view of left ear region. Stereophotograph. See fig. 18 for key.

high. It is probable that the basioccipital tubercle was closer to the occipital condyle and was not completely separated from it in *Australochelys* as it is in *Proganochelys.*

The foramen magnum in *Proganochelys* is wider than high and in *Australochelys* it is vice versa, possibly made more so by deformation.

A clearly defined fenestra ovalis (figs. 17, 18) is present on both sides of the skull in *Australochelys* in the same relative position in *Proganochelys.* The fenestra ovalis in *Australochelys* is oriented more vertically than in *Proganochelys.*

In *Australochelys* opisthotic sutures can be discerned distally only, but the areas presumably representing the opisthotics are preserved on both sides of the skull (figs. 15–18). In *Proganochelys* the bar of bone between the fenestra ovalis and the foramen jugulare anterius, which is the area where the processus interfenestralis is developed in Casichelydia, is very low. In *Australochelys* this bar is considerably deeper, separating those openings by a ridge of bone. This is still far from the definitive processus interfenestralis found in casichelydians where a recessus scalae tympani and fenestra perilymphatica are formed, but it does seem to approach that condition.

The foramen jugulare anterius in *Australochelys* (figs. 11, 15–18) is very similar to that opening in *Proganochelys,* but it is more deeply surounded by bone. Nonetheless, a definitive foramen jugulare posterius of the casichelydian type is not present.

The processus paroccipitalis of the opisthotic in *Australochelys* (figs. 19–22) differs from that in *Proganochelys* in having a ventral ridge, developed medially between the fenestra ovalis and foramen jugulare anterius, and extending for the entire length of the processus paraoccipitalis. Distally, the opisthotic is covered, presumably by the squamosal and quadrate.

No sutures are visible delimiting the basisphenoid in *Australochelys,* but the presumed area of the basisphenoid is preserved (figs. 15, 16). The ventral surface of the bone forms a midline trough, in contrast to the midline ridge seen in *Proganochelys.* In casichelydians the basisphenoid is generally flat ventrally. Anteriorly, *Australochelys* has a blunt cultriform process in comparison to *Proganochelys,* but it may have been made more blunt by postmortem damage. None-

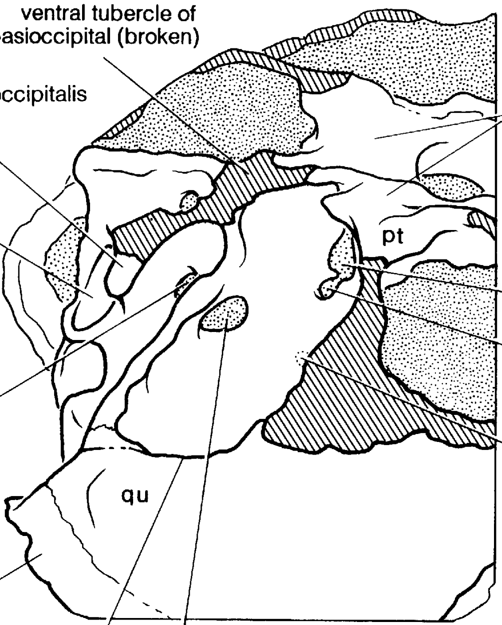


Fig. 18. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Ventrolateral oblique view of the left ear region.

theless, it is closer to the casichelydian reduced or absent cultriform process than to the elongate condition of *Proganochelys*. On either side of the base of the cultriform process in *Australochelys*, the presumed basisphenoid curves ventrolaterally to the pterygoid (figs. 15, 16). This area is open and has no contact in *Proganochelys*, but in *Australochelys* and the Casichelydia it is part of the sutured, akinetic joint between basisphenoid and pterygoid.

Posteriorly in *Australochelys* the basisphenoid has paired basipterygoid processes that contact and are indistinguishably fused to the pterygoids. Thus, in addition to the fused basipterygoid articulation, akinesis in *Australochelys* also involves a broad contact of pterygoid and basisphenoid for most of the length of the basisphenoid.

Despite all efforts, neither carotid foramen could be found. A number of cracks and fissures filled with hematite were probed, but none seem to have formed margins. However, this is consistent with the type of preservation present in *Australochelys* in which fine detail is lost. Any of these cracks could be the carotid foramina.

RELATIONSHIPS

The characters relevant to determining the relationships of *Australochelys* are listed in table 2. They are discussed below in the same order as presented in the table. Further information on each character can be found in the descriptive section, which is also arranged in the same order.

1. Apertura narium externa united: 0 = apertura narium externa divided by premaxillae; 1 = apertura narium externa united.—The paired nasal openings divided by dorsal premaxillary processes are primitive tetrapod features found in *Proganochelys*. *Australochelys* has divided aperturae, but the bone is only presumed to be premaxilla. In *Kayentachelys* the nares are united as in most other turtles. Forms such as *Meiolania* (Gaffney, 1983) and *Kallokibotion* (Gaffney and

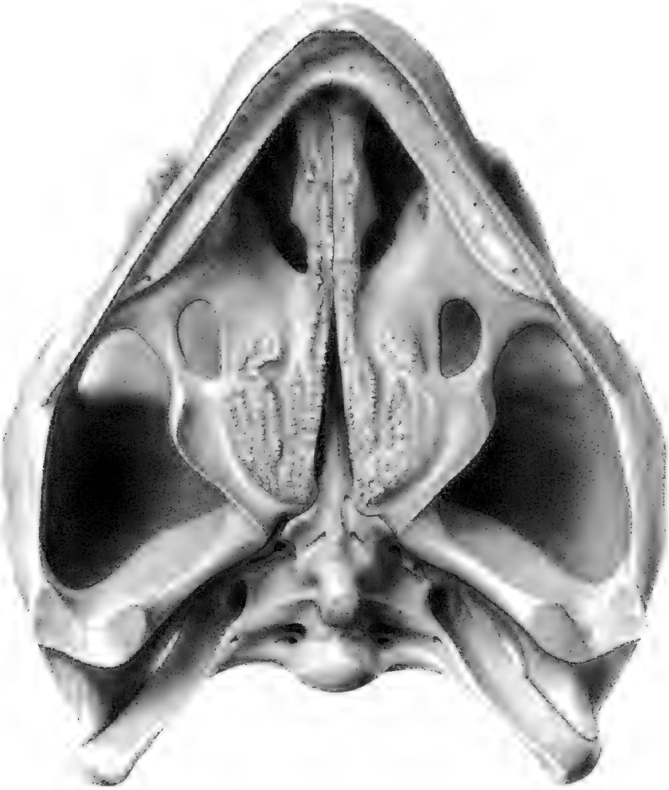


Fig. 19. *Proganochelys quenstedti,* ventral view of skull, from Gaffney, 1990.

Meylan, 1992) have divided nares, but not due to dorsal processes of the premaxillae, the primitive condition. This character is interpreted as a casichelydian synapomorphy.

2. Apertura narium externa elongate: 0 = apertura narium externa oval or wide; 1 = apertura narium externa elongate.—*Australochelys* is unique in possessing this feature and we interpret it as an autapomorphy. It is quite likely associated with the generally large size of the fossa nasalis in this form.

3. Lacrimal foramen present: 0 = lacrimal foramen present; 1 = lacrimal foramen absent.—The lacrimal foramen is primitive for turtles. It is present in *Proganochelys* as well as *Australochelys. Australochelys* differs from *Proganochelys* in having an unusually large foramen. This is a presumed autapomorphy, as the foramen is generally smaller in more primitive tetrapods. The absence of the lacrimal foramen is interpreted as a casichelydian synapomorphy.

4. Orbit very large: 0 = orbit variable but usually small; 1 = orbit very large.—*Australochelys* is unique among turtles in having a huge fossa orbitalis. This is an *Australochelys* autapomorphy. The orbit is also large in *Proganochelys,* but it is within the range seen in sea turtles and is therefore not a good synapomorphy with *Australochelys.*

5. Cranial sutures fused: 0 = sutures not fused; 1 = sutures fused.—This character occurs sporadically in turtles and in other amniotes and is very difficult to homologize using morphologic tests. It is probably common to adults of both *Proganochelys* and *Australochelys,* but its sporadic distribution (e.g., baenids, *Platysternon, Emydura*) in other turtles causes us to reject it as a synapmorphy.

6. Posterior margin of temporal roof extends past opisthotic in dorsal view: 0 = temporal roof anterior to opisthotic; 1 = temporal roof posterior to opisthotic.—Because this condition occurs in *Australochelys, Kayentachelys,* and *Kallokibotion* (Gaffney and Meylan, 1992), we interpret it as a rhapto-

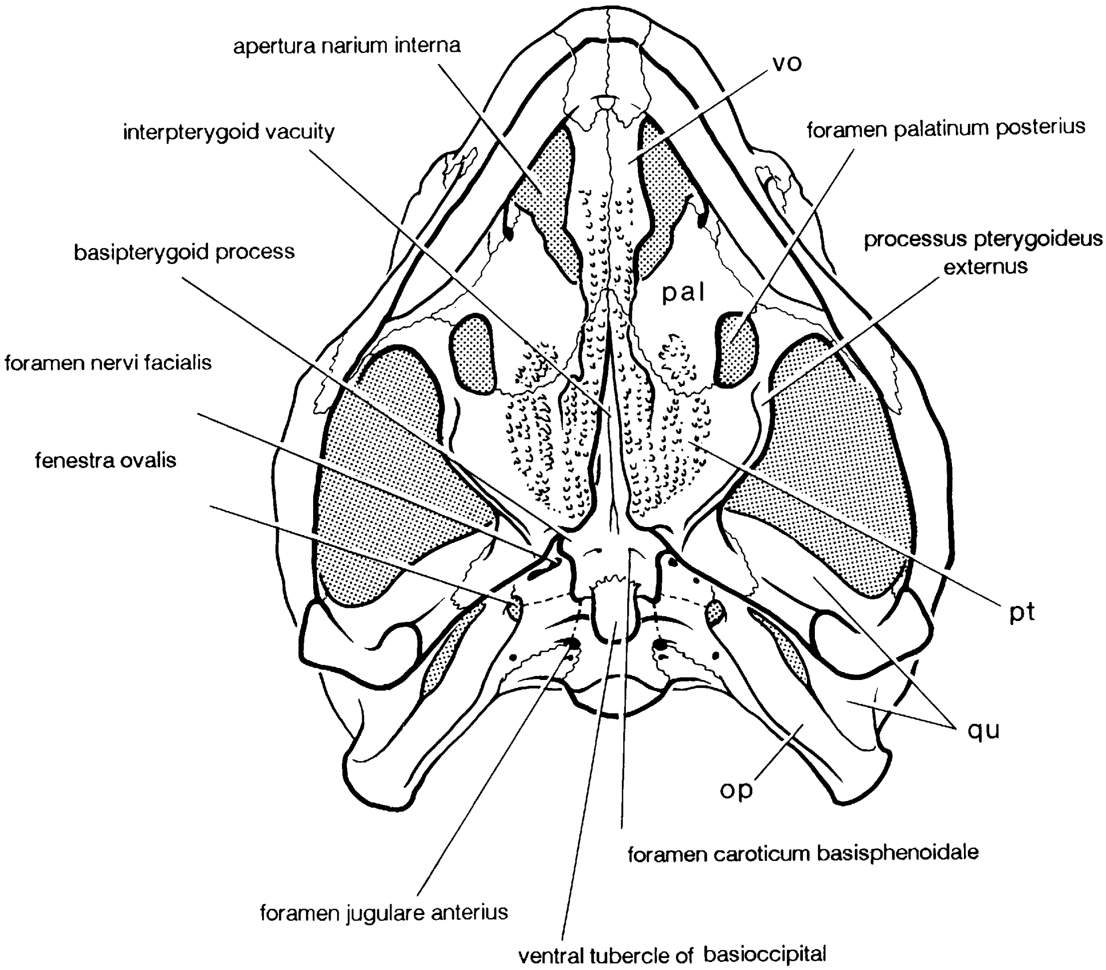


Fig. 20. *Proganochelys quenstedti,* ventral view of skull, redrawn from Gaffney, 1990.

chelydian synapomorphy (i.e., uniting *Australochelys* and Casichelydia). Other turtles that have posteriorly extensive skull roofs have constituent bones with different proportions, which suggests that the *Kayentachelys* condition is primitive for cryptodires. We do not know with certainty what bones make up the temporal roof in *Australochelys.* For the present, it seems best to use this condition as a rhaptochelydian synapomorphy.

7. Triturating surfaces narrow: 0 = triturating surfaces narrow; 1 = triturating surfaces narrow and wide.—The widths of jaws in turtles vary a great deal, but narrow jaws seem to be the primitive condition at least at the level of Testudines. Because all outgroups for turtles have narrow, toothed jaws, it is hard to make outgroup comparisons here and we conclude that the use of this feature is unclear.

8. Vomers highly arched dorsally, narrow posteriorly, broad anteriorly: 0 = vomers relatively horizontal; 1 = vomers highly arched.—The morphology of the anterior end of the palate in *Australochelys* is very unusual and is here interpreted as an autapomorphy.

9. Palatal teeth few or absent: 0 = palatal teeth present (vomerine teeth present); 1 = palatal teeth few or absent (vomerine teeth absent).—Although we are not able to resolve the question of palatal teeth in *Australochelys,* many teeth on the palatal surface clearly were not present, as in *Proganochelys.* We interpret this reduction or absence of palatal teeth, particularly the absence of teeth on the vomer, as a rhaptochelydian synapomorphy.

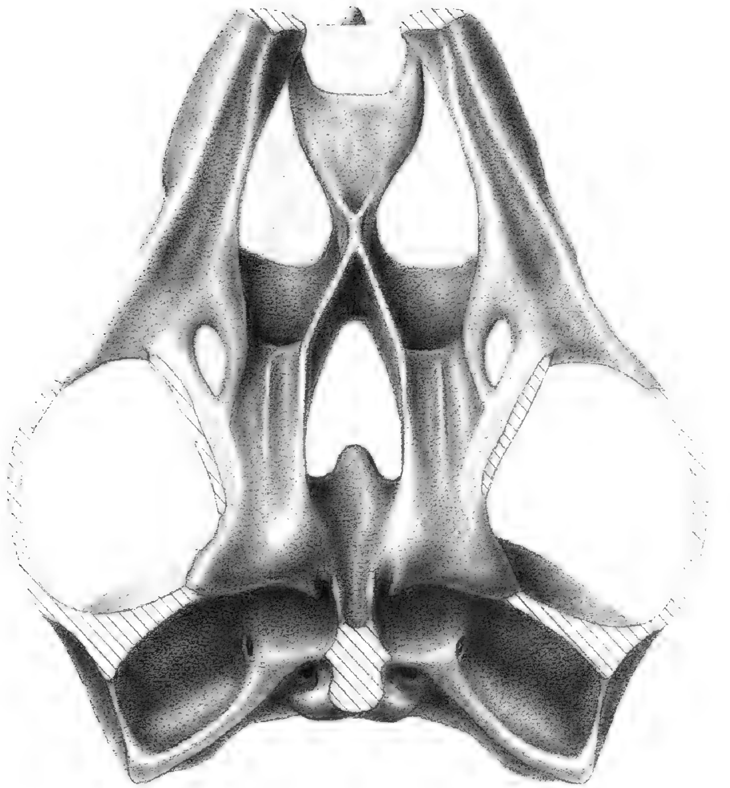


Fig. 21. *Australochelys africanus*, ventral view of skull.

10. Basipterygoid articulation sutured: 0 = basipterygoid articulation a movable joint; 1 = basipterygoid articulation sutured.—This is considered to be the most important feature relating *Australochelys* to casichelydians. The loss of kinesis of the palatoquadrate elements in the turtle braincase was closely correlated with a number of reorganizational changes in the turtle skull involving the origin of the cryptodires and pleurodires (Gaffney, 1975, 1979). The morphology of the contacting elements in turtles differs significantly from the morphology in other groups that have developed akinesis (e.g., temnospondyls, pareiasaurs, therapsids, archosaurs).

11. Cultriform process present: 0 = cultriform process present; 1 = cultriform process absent.—The persistence of a visible cultriform process and related large interpterygoid vacuity are interpreted as primitive features retained in *Australochelys* and lost in Casichelydia. We consider the small or closed interpterygoid vacuity and the absence of a cultriform process as casichelydian synapomorphies.

12. Large interpterygoid vacuity: 0 = interpterygoid vacuity large; 1 = interpterygoid vacuity small or absent.—See character 11.

13. Cranioquadrate space a well-defined canal: 0 = cranioquadrate space open; 1 = cranioquadrate space closed to a canal.—In *Proganochelys* and generalized tetrapods the cranioquadrate space is relatively open. In casichelydians it is closed, resulting in a canal or canals for the enclosed structures. *Australochelys* is united with casichelydians in having the cranioquadrate space reduced to a foramen (presumably leading into a canal) for the lateral head vein, the canalis cavernosus (Gaffney, 1979, 1983). This condition seems to be correlated with the loss of mobility at the basipterygoid articulation, but this is not always the case in other akinetic taxa. We interpret this character as a relatively well-tested rhaptochelydian synapomorphy.

14. Stapes thin and articulates with a tympanic membrane: 0 = stapes heavy and articulates with a concavity on the quadrate; 1 = stapes thin and articulates with a tympamic

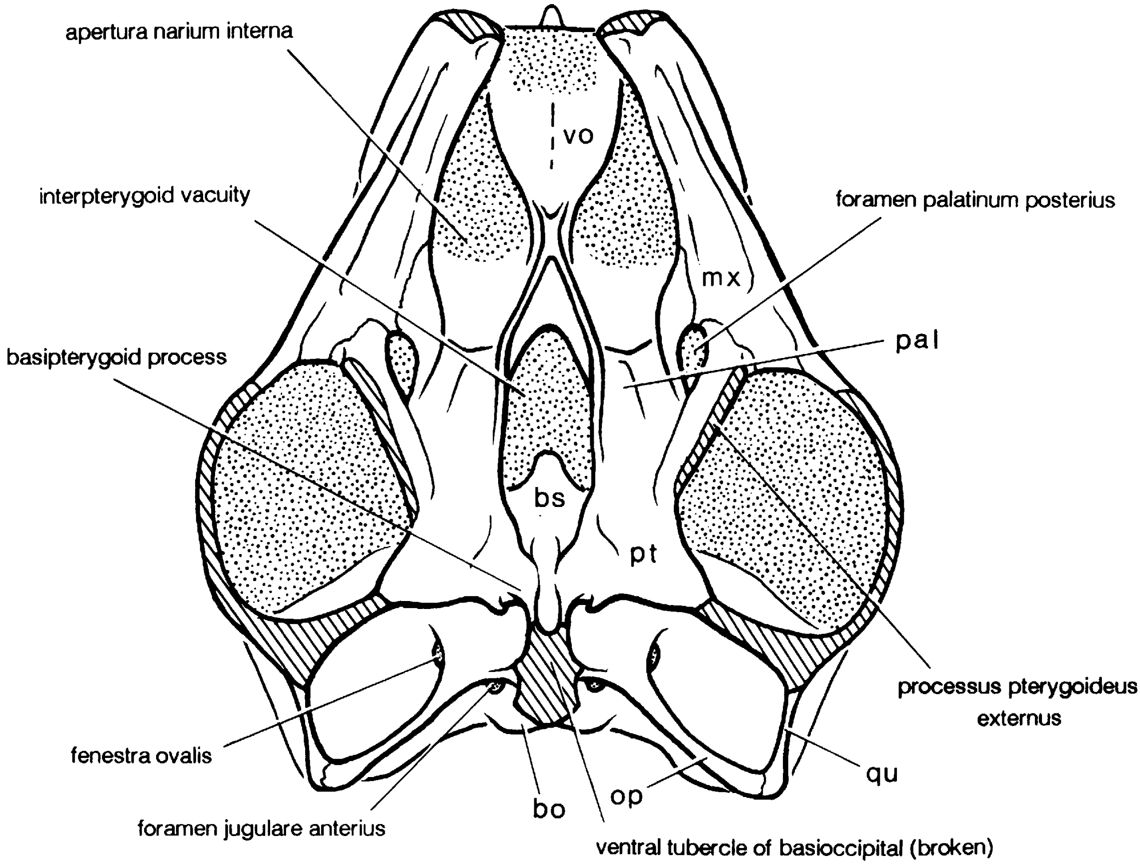
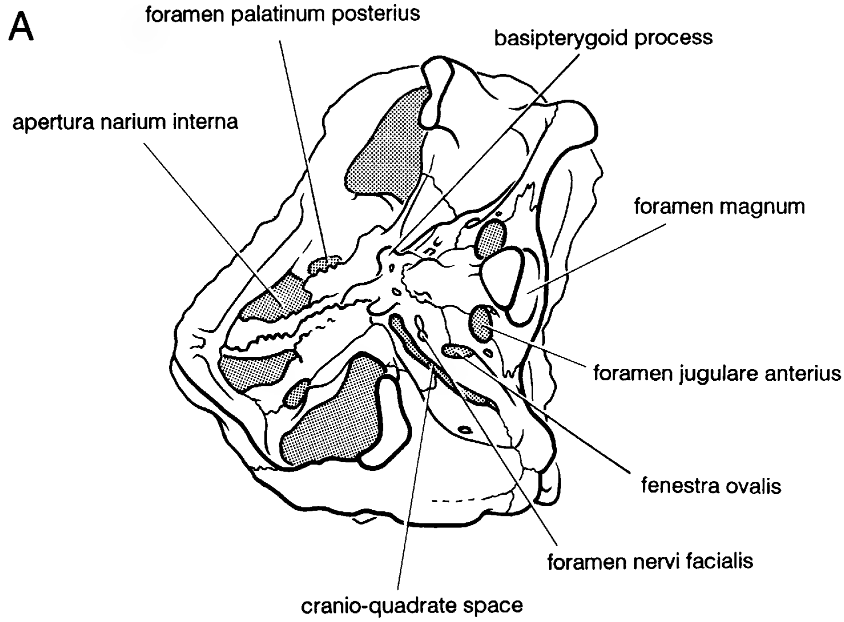


Fig. 22. *Australochelys africanus,* ventral view of skull.

membrane.—As described in Gaffney (1990), the stapes of *Proganochelys* is a stout, relatively heavy column that extends from the fenestra ovalis to a distinct concavity on the quadrate where the distal end of the stapes articulates. In pleurodires and cryptodires the stapes is much thinner, particularly distally, where it contacts the tympanic membrane. In *Kayentachelys* the stapes is not preserved, but the position of the fenestra ovalis and the shape of the quadrate, which lacks a stapedial articulation concavity, indicate a stapes that articulates with the tympanum. Similarly, in *Australochelys* the stapes is not preserved, but there is no stapedial articulation concavity on the quadrate and the stapes probably articulated with a tympanic membrane. In any case, the light stapes is a casichelydian synapomorphy that is circumstantially, but not definitely, present in *Australochelys.*

15. Quadrate with acute ridge on posterior margin: 0 = ridge absent; 1 = ridge or well-developed flange present.—In casichelydians the quadrate has a large, posterior flange that separates the well-defined cavum tympani from the more medial middle ear region and forms the unique, funnel-shaped quadrate of living turtles. *Proganochelys* lacks the flange and has only a curved, C-shaped quadrate, not funnel-shaped. *Australochelys* also lacks the large quadrate flange that forms the definitive funnel-shaped cavum tympani, but it does seem to be advanced over *Proganochelys.* The *Australochelys* quadrate has a vertical ridge along its posterior edge that we interpret as an early stage of development of the larger quadrate flange seen in casichelydians.

16. Funnel-shaped cavum tympani present: 0 = funnel-shaped quadrate absent; 1 = funnel-shaped quadrate present.—*Proganochelys* and *Australochelys* lack the funnel-shaped, recessed cavum tympani formed by a large quadrate flange as seen in casichelydians. This character could be interpreted as a more advanced state of the previous char-



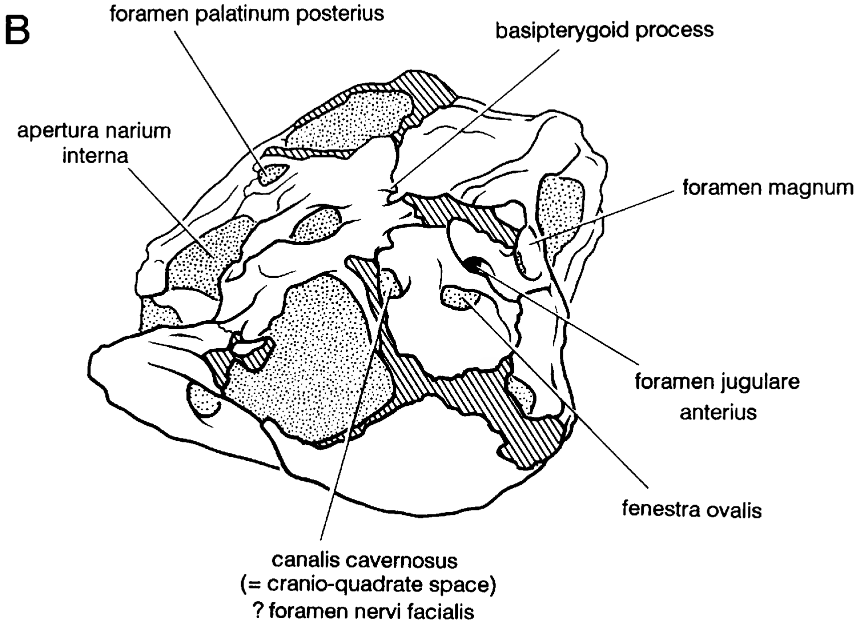


Fig. 23. Comparison of ear regions in posterior oblique views. Anterior is to the left. **A.** *Proganochelys quenstedti,* redrawn from Gaffney, 1990. **B.** *Australochelys africanus.*

acter, although we prefer to use only two-state characters.

17. Ventral ridge on opisthotic present: 0 = ventral ridge on opisthotic absent; 1 = ventral ridge on opisthotic present.—This is another character common to casichelydians and *Australochelys,* though it is modified in various ways within casichelydians. The ventral ridge is another component of an enclosed middle ear region, that is absent in *Proganochelys* but present in *Australochelys.*

18. Distal end of opisthotic covered by

Fig. 24. *Australochelys africanus* Gaffney and Kitching, 1994, BP/1/4933. Shell fragment, probably from the bridge area, exposed only in internal view. Orientation not determined.

squamosal and/or quadrate: 0 = opisthotic not covered; 1 = opisthotic covered.—This feature, which is held in common by *Australochelys* and casichelydians, is related to the expansion of the cavum tympani in casichelydians. In *Australochelys* it is only a relatively slight increase of the dermal bone covering in the upper part of the tympanic region.

19. Paroccipital process of opisthotic tightly sutured to quadrate and prootic: 0 = process separated from prootic and quadrate; 1 = process tightly sutured to prootic and quadrate.—In *Proganochelys,* as in more generalized tetrapods with the primitive form of cranial kinesis (Gaffney, 1990), the paroccipital process lies against the quadrate and prootic with a relatively open fissure separating much of their length. *Australochelys* and casichelydians have this space completely closed with no possible movement of the paroccipital process. Along with other features consistent with the loss of kinesis in *Australochelys* and Casichelydia, we interpret this character as a synapomorphy uniting these groups.

20. Foramen jugulare posterius formed in bone: 0 = foramen jugulare posterius completely absent; 1 = at least medial edge of foramen jugulare posterius formed by exoccipital.—In *Proganochelys* and *Australochelys* the foramen jugulare anterius is the foramen seen in occipital view. In casichelydians it is a secondary foramen, the foramen jugulare posterius, that is visible in occipital view. Even though some casichelydians, such as baenids, may have an incomplete foramen jugulare posterius, they still have at least the medial edge formed by a flange from the exoccipital. This character is closely related to the following character.

21. Recessus scalae tympani and fenestra perilymphatica formed in bone: 0 = not defined by bone; 1 = defined by bone.—Possibly related to the formation of this secondary foramen, the foramen jugulare posterius, is the peculiarly chelonian fenestra perilymphatica and recessus scalae tympani (Gaffney, 1979). All these features occur only in casichelydians and are interpreted as synapomorphic for that group.

22. Ventral basioccipital tubercle: 0 = tubercle absent; 1 = tubercle present.—Both *Proganochelys* and *Australochelys* have a well-developed tubercle on the ventral side. The tubercle does not occur in any other turtles. It also does not occur in any likely turtle outgroups, such as procolophonids, *Owenetta,* pareiasaurs, or captorhinids. As far as can be determined, the morphology of the tubercle is the same in *Australochelys* and *Proganochelys.* Because the hypothesis that *Australochelys* is more closely related to casichelydians than to *Proganochelys* is most parsimonious under our analysis, the tubercle would be interpreted as homoplastic and presumably lost in casichelydians.

23. Crista supraoccipitalis is a distinct vertical sheet of bone: 0 = crista supraoccipitalis absent or small; 1 = crista supraoccipitalis distinct vertical sheet.—The crista supraoccipitalis is *Proganochelys* is a small ridge. In *Australochelys* it is a distinct, thin sheet of

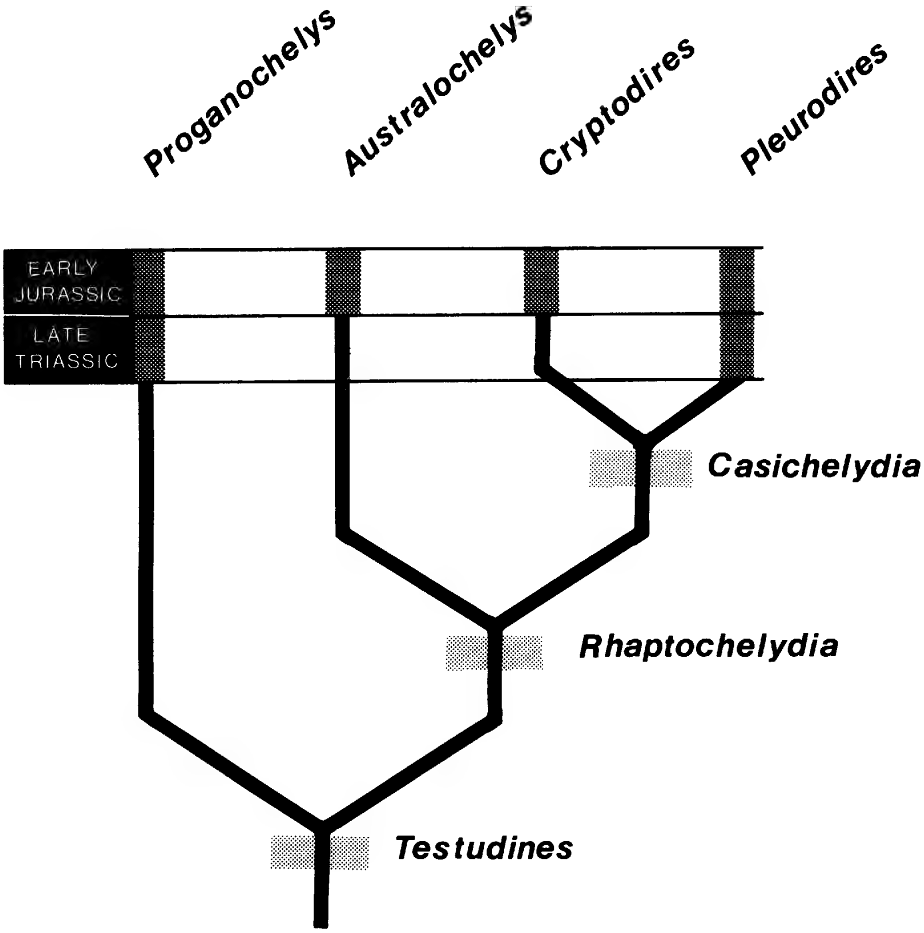


Fig. 25. Relationships of *Australochelys* with geologic ranges of taxa indicated. Diagnoses of higher taxa are in the text.

bone extending ventrally from the skull roof and separating the cavum cranii proper from the skull roof. In casichelydians the crista supraoccipitalis is deeper and posteriorly more extensive, but is clearly similar to that in *Australochelys.* We interpret this as a rhaptochelydian synapomorphy.

24. Lateral edge of pterygoid without lateral processes: 0 = edge of pterygoid downturned, without lateral processes; 1 = edge of pterygoid with lateral process.—In *Proganochelys* and probably *Australochelys* the lateral margin of the pterygoid lacks lateral processes and is downturned or rolled with a low ridge along the margin. The conditions in possible outgroups for this character vary considerably, but none has lateral processes. The *Australochelys* condition is in doubt because most of the preserved edges are broken. Nonetheless, this may be interpreted as a common feature in *Proganochelys* and *Australochelys.* It is most likely a primitive character at the level of Testudines.

The above list indicates nine characters interpreted as synapomorphies of *Australochelys* and Casichelydia (6, 9, 10, 13, 15, 17–19, 23). This contrasts with two characters (4, 22; possibly three, if 24 is included) that unite *Australochelys* with *Proganochelys.* There are no derived characters in *Australochelys* that link it with pleurodires or cryptodires separately. Even without a computer-run parsimony analysis, it is clear that the characters support only one tree with *Australochelys* as the sister group of Casichelydia and *Proganochelys* as the sister group of *Australochelys*

TABLE 2
Comparison of *Australochelys* with Other Turtles

Character	Primitive tetrapod	*Proganochelys*	*Australochelys*	*Casichelydia*
1. Apertura narium externa united	No	No	No	Usually yes
2. Apertura narium externa elongate	No	No	Yes	No
3. Lacrimal foramen	Present, small	Present, small	Present, large	Absent
4. Orbit size	Variable	Large	Very large	Variable
5. Cranial sutures fused	Usually no	Probably in adults only	Yes	Usually no
6. Posterior margin of temporal roof extends over opisthotic	No	No	Yes	Primitively yes
7. Triturating surfaces narrow	Variable	Yes	Yes	Primitively yes
8. Vomers highly arched dorsally, narrow posteriorly, broad anteriorly	No	No	Yes	No
9. Palatal teeth	Many	Many	Few or absent	Few or absent
10. Basipterygoid articulation sutured	No	No	Yes	Yes
11. Cultriform process	Present	Present	Present	Absent
12. Large interpterygoid vacuity	Yes	Yes	Yes	No
13. Cranioquadrate space a well-defined canal	No	No	Yes	Yes
14. Stapes thin and articulates with tympanic membrane	No	No	Probably yes	Yes
15. Quadrate with acute ridge on posterior margin	No	No	Yes	Primitively yes
16. Recessed, funnel-shaped cavum tympani	Absent	Absent	Absent	Present
17. Ventral ridge on opisthotic	No	No	Yes	Yes
18. Distal end of opisthotic covered by squamosal/quadrate	No	No	Yes	Yes
19. Paroccipital process of opisthotic tightly sutured to braincase	No	No	Yes	Yes
20. Foramen jugulare posterius formed in bone at least medially	No	No	No	Yes
21. Recessus scalae tympani and fenestra perilymphatica defined by bone	No	No	No	Yes
22. Ventral basioccipital tubercle	Absent	Present	Present	Absent
23. Crista supraoccipitalis a distinct vertical sheet of bone	No	No	Yes	Yes
24. Lateral edge of pterygoid	Variable, no lateral process	Downturned, no lateral process	Probably downturned, no lateral process	Variable but with lateral process

plus Casichelydia. The conflicting characters uniting *Proganochelys* and *Australochelys* would be interpreted as primitive for turtles that were lost once rather than having originated twice.

The skulls of Recent turtles are highly modified over the generalized amniote condition. However, such forms as *Proganochelys* and *Australochelys* and other fossils do provide important glimpses of how the more derived conditions evolved. The significance of *Australochelys* is that it gives a view of the turtle skull well after the origin of turtles but before the origin of the modern groups, when the themes of akinesis and middle ear modification were just beginning.

Akinesis has evolved independently in a number of amniotes, with mammals being the most prominent among the Recent fauna. As discussed elsewhere (Gaffney, 1990), the primitive chelonian skull was kinetic in the sense of a movable basipterygoid articulation

as retained from the generalized amniote condition, and does not necessarily mean that palatoquadrate/braincase movement actually took place. *Proganochelys* has this generalized condition of kinesis; all other turtles are akinetic. Living cryptodires and pleurodires have extensive bony processes and sutured contacts that obliterate the open areas and sliding contacts of the primitive condition (Gaffney, 1975). *Australochelys* is akinetic in having a fused basipterygoid articulation and an expanded basisphenoid–pterygoid contact but lacks other features of casichelydian akinesis. The evolutionary reasons for the development of akinesis are speculative. The condition clearly affects nearly every cranial system, especially the feeding mechanism and the auditory system. Turtles had already evolved a beak before akinesis, but the trochlear jaw mechanism did not appear until cryptodires and pleurodires were differentiated. In *Australochelys* the feeding mechanism appears to be virtually the same as in *Proganochelys.*

The auditory system, however, is clearly different between *Proganochelys* and *Australochelys,* and this change is probably related to akinesis. The kinetic skull of *Proganochelys* has an open, slit-shaped cranioquadrate space between the braincase and the palatoquadrate. The middle ear region is relatively open and has anterior and medial walls that could be movable with respect to one another. In *Australochelys* the cranioquadrate space is replaced by a foramen or foramina for the included structures and the space is largely filled by bony contacts between palatoquadrate and braincase. The middle ear region of *Australochelys* is more ossified and enclosed than in *Proganochelys.* Whether this is a consequence or a precursor of akinesis is not known, nor is the function of this ossification and enclosure known. It seems likely that the hypertrophy of the middle ear region preceded the origin of the jaw muscle trochleas (Gaffney, 1975) and that akinesis and otic chamber hypertrophy are related to each other.

The Casichelydia was originally erected by Gaffney (1975) for all turtles except *Proganochelys* because they had a series of derived characters in common, including akinesis. The Casichelydia could be redefined to include *Australochelys,* but we have chosen to retain Casichelydia as cryptodires plus pleurodires and redefine it with the derived characters in the following diagnosis:

CASICHELYDIA

DIAGNOSIS: Apertura narium externa united, not separated by premaxillary processes as in *Proganochelys*; lacrimal bone and foramen absent; cultriform process absent; interpterygoid vacuity small or absent; cavum tympani well developed and recessed into a funnel-shaped bony structure; a definitive foramen jugulare posterius formed in bone, at least medially, in contrast to *Proganochelys* and *Australochelys*; recessus scalae tympani and fenestra perilymphatica defined by bone.

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